THE CONDOR

Volume 59 May-June, 1957 Number 3

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

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Published bi-monthly at Berkeley, California. Entered as second-class matter at the post office at Berkeley, California, May 15, 1925, under Act of Congress of March 3, 1879. Issued from the office of THE CONDOR, Museum of Vertebrate Zoology, Berkeley 4, California.

MANUSCRIPTS

Send manuscripts for publication to the Editor, ALDEN H. MILLER, Museum of Vertebrate Zoology, Berkeley 4, California, or to the Associate Editor, FRANK A. PITELKA, same address. Refer to suggestions on preparation of manuscripts for THE CONDOR on the back cover of recent issues of the journal.

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Subscription price to non-members, five dollars per volume, payable in advance. Single copies, one dollar each.

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Issued May 24, 1957

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TORPIDITY IN THE WHITE-THROATED SWIFT, ANNA HUMMINGBIRD, AND POOR-WILL

By GEORGE A. BARTHOLOMEW, THOMAS R. HOWELL, and TOM J. CADE

In recent years there has been considerable interest in torpidity and reduced body temperature or hypothermia among birds. The hibernation (Jaeger, 1948, 1949, 1952; Thorburg, 1953; Marshall, 1955) of the Poor-will (*Phalaenoptilus nuttallii*), the nocturnal torpidity (Huxley, Webb, and Best, 1939; Pearson, 1950, 1953) of hummingbirds, and the labile temperatures (Koskimies, 1948) of the European Swift (*Apus* (*Micropus*) *apus*) have shown that constant high temperature is not an invariable rule even among adult birds. The present study provides quantitative data on hypothermia for two species previously investigated, the Poor-will and the Anna Hummingbird (*Calypte anna*), and information on a hitherto unstudied member of the Apodiformes, the White-throated Swift (*Aëronautes saxatalis*).

MATERIALS AND METHODS

We attempted to obtain simultaneous records of body temperatures and metabolic rates under controlled environmental conditions. Temperatures were measured with silver-soldered thermocouples made of 30-gauge copper-constantan duplex wire and were recorded to the nearest tenth of a degree C. on a recording potentiometer. Environmental or ambient temperatures were controlled within one degree C. by an insulated chamber equipped with heating and cooling units, a fan, lights, and an insulated glass port for observation.

Oxygen consumption was used as a measure of metabolic rate. During the experiments, air was metered through a chamber containing the bird and was delivered to a Beckman paramagnetic oxygen analyzer which, in conjunction with a recording potentiometer, provided a continuous record of oxygen consumption. All volumes of oxygen have been corrected to 0°C. and a pressure of 760 mm. Hg.

WHITE-THROATED SWIFT

The White-throated Swift is abundant over western North America and ranges south through México into Guatemala and El Salvador. It is migratory in the northern part of its range and winters from west-central California south at least into México. The usual roosting and nesting sites are crevices in rocky cliffs.

For the present study, 19 swifts were captured at a roosting site in a cliff about two miles southeast of Lompoc, Santa Barbara County, California, on February 26, 1956. The birds were banded and divided into three groups. Eight were placed in the dark at 4 to 5°C. without food, four were placed in the dark at 20 to 22°C. without food, and seven were kept under 12 hours of light and 12 hours of darkness at 20 to 22°C. The latter birds were fed beef heart, *Tenebrio* larvae, water, and powdered multivitamin capsules. The swifts were fed by hand about four times per day during the light period. They soon learned to seize food morsels presented to them and seemed to eat well, but their body weights declined steadily in the week that they were kept. Water administered by pipette, usually alternated with food morsels, was taken readily. The swifts were docile and easy to handle. They rarely attempted to fly but crawled and climbed

easily and rapidly. At rest they tended to huddle together at the top of the cage, often crowding in so closely that they overlapped one another like shingles.

Body temperatures before experimentation.—The swifts were captured at sundown and immediately put into a large sack. About five hours later, they were removed and placed in cages in the laboratory at the University of California at Los Angeles. The birds huddled closely together in the sack, and a quick-registering mercury thermometer inserted into the mass of swifts recorded a temperature of 37.3°C. (room temperature about 20°C.). Individual cloacal temperatures at this time ranged from 35.6 (one bird away from the huddled mass) to 41.0°C. (average 38.6°C.).

Weight.—Individual weights taken five hours after capture ranged from 29.0 to 33.5 gm. (average 30.5 gm.). No segregation by sex was possible as there are no external sexual differences in this species.

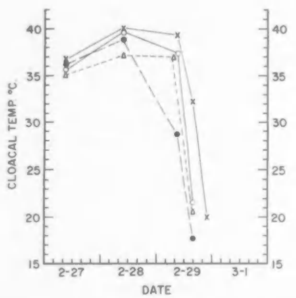

Fig. 1. Cloacal temperatures in unfed White-throated Swifts maintained in the dark at 4–5°C. Experiment was terminated at last readings shown. All four birds subsequently aroused completely.

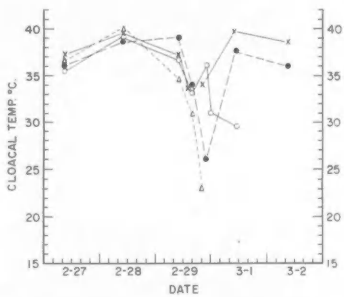

Fig. 2. Cloacal temperatures in unfed White-throated Swifts maintained in the dark at 20–22°C.

In darkness, unfed, at 4 to 5°C.—Eight birds were subjected to these conditions starting at 12 noon on February 27, 18 hours after capture. Three birds died within 45 hours, and a fourth died about 25 hours later. These four birds maintained high body temperatures for at least the first 22 hours, and the one that survived longest had a high temperature at the 45-hour reading. We do not know whether or not the birds experienced prolonged hypothermia before death. The four remaining birds became hypothermic on the third day of the experiment (fig. 1), and all subsequently returned to the active range of body temperature (see section on arousal).

In darkness, unfed, at 20 to 22°C.—The four birds subjected to this treatment maintained high body temperatures for about 48 hours (fig. 2). Six hours later there was a marked drop in body temperature. Subsequently one bird failed to recover, one made a partial recovery, and two returned to normally high body temperatures (fig. 2).

Twelve hour photoperiod, fed, at 20 to 22°C.—Birds kept under these conditions maintained high body temperatures for at least 72 hours (fig. 3), during which time some of them were subjected briefly to ambient temperatures down to 12°C. All seven of the birds in this group showed a steady loss in weight despite our efforts to feed them adequately, and two of them died. By the fifth day after capture, the five surviving birds showed markedly depressed body temperatures (fig. 3), and four readily roused from this hypothermic state. The four that survived were those that had best maintained

their body weight. One of these had damaged wing feathers and could not fly, but the others were released a few hours after arousal from hypothermia. All three birds flew off at once, and two that remained in view began catching insects in a normal manner. It therefore seems reasonable to assume that these swifts had recovered fully.

Arousal from hypothermia.—Body temperatures of fed and unfed birds were measured during arousal from hypothermia at both 4 to 5°C. and 20 to 22°C. (fig. 4). No differences were evident in rate of arousal in fed and unfed birds; arousal was as rapid at 4 to 5°C. as at 20 to 22°C. A rise in body temperature of about 0.4°C. per minute was typical. Some birds underwent as many as four cycles of hypothermia and arousal in the course of the experiments.

During hypothermia the birds kept their body plumage fluffed out, and they clung strongly to anything with which their feet were in contact—usually a vertical side of the cage.

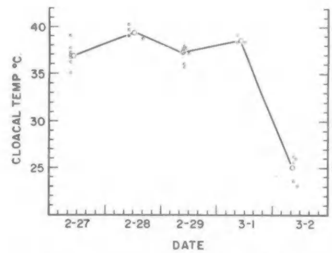

Fig. 3. Cloacal temperatures in fed White-throated Swifts maintained on a 12-hour photoperiod at 20–22°C. The large circles indicate mean temperatures.

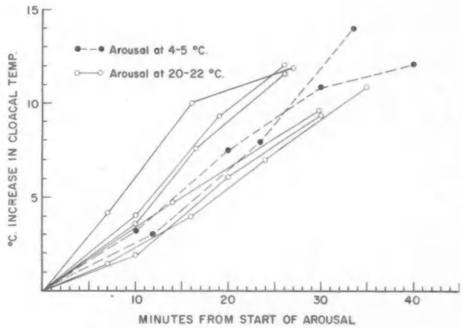

Fig. 4. Increase in cloacal temperature in White-throated Swifts during arousal from torpor. All starting temperatures were between 20 and 26°C.

Behavior of nine different birds during arousal is summarized in table 1. The lowest body temperature from which swifts subsequently returned to normal was 20.0°C., but some birds survived for at least four hours at body temperatures between 15.8 and 20°C. As shown in table 1, swifts were capable of effective, coordinated movement at body temperatures as low as 25.8°C., and at body temperatures of 35°C. their activity appeared to be normal. The lowest body temperature at which spontaneous flight was observed was 36.2°C.

Table 1

Summary of Behavior of Nine Swifts During Arousal at 20–22°C.

Cloacal temperature, °C.	Behavior
15.8	Alive, but completely motionless and unresponsive.
17.7–20.5	Moves wings and feet slightly; no corneal reflex; cannot right, but clings with feet; eyes closed.
22.0–24.0	Elevates wings vertically when touched; crawls slowly; eyes open.
24.0	First visible shivering; still crawls slowly.
25.8–35	Strong shivering, vigorous crawling and climbing; wings fluttered at 31.0°C.
35–41	Alert and normal, able to fly.

It was difficult to obtain satisfactory oxygen consumption readings from the swifts as the birds rarely remained quiet while in the respirometer. However, one bird with a body temperature of 37.9°C. at an environmental temperature of 20°C. remained inactive for several hours and consumed oxygen at an average rate of 5.2 cc./gm./hr.

ANNA HUMMINGBIRD

This species, which is a common resident in most of California, has previously been shown to undergo torpidity (Pearson, 1950). On December 13, 1955, an adult male Anna Hummingbird that had flown into the University Library was captured at 10:30 a.m., not more than two hours after its entry. Its weight was 4.6 gm., its deep esophageal temperature was 41.9°C., and it appeared to be in perfect condition. At 11:30 a.m. the bird was placed in the respirometer and its oxygen consumption was measured for 22

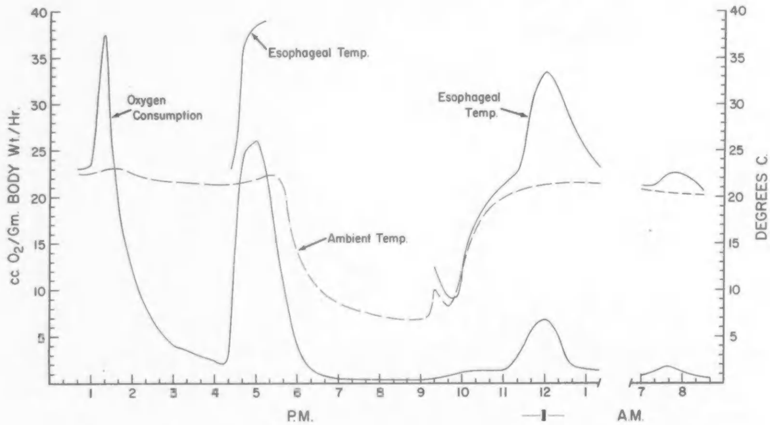

Fig. 5. Oxygen consumption and body temperature in an adult male Anna Hummingbird exposed to varying ambient temperatures.

consecutive hours. For about 13 of these hours, a continuous record of body temperature was obtained from a thermocouple placed 5 to 10 mm. down the bird's esophagus and secured to its culmen. In the course of the experiment, the ambient temperature was varied through a range of 16°C. The bird was not given food or water at any time.

On August 10, 1956, an immature Anna Hummingbird of unknown sex was obtained. It had a broken leg and an injured wing; how long it had been without food is not known, but it weighed only 2.65 gm. at the time of capture. This bird was maintained by feeding it a mixture of water, honey, cane sugar, and gelatin, and its responses to various low ambient temperatures were measured.

The measurements obtained from the adult male hummingbird are summarized in figure 5; those obtained from the immature bird are given in figure 6. The adult male became torpid at an ambient temperature of 21 to 23°C. and also as ambient temperature declined from 23 to 7°C. (fig. 5). The immature bird became torpid at an ambient temperature of 2°C. and also at 23°C. during the night in its cage (body temperature 26°C.).

Entry into torpor was marked by a steady decline in oxygen consumption and body temperature (figs. 5 and 6). As the birds became torpid, they sat quietly with eyes closed, feathers fluffed out, and bill pointed upward at an angle of about 45°. We recorded a body temperature as low as 8.8°C. (ambient temperature 8.2°C.) in the adult bird, and at that time it was completely motionless. When the bird was handled at a body temperature of 12°C., it uttered a few faint "peeps" and spread the rectrices widely, but it slumped to one side and lay motionless when set down. When the immature bird was handled at a body temperature of 15.5°C., it spread its wings and waved them slowly. At a body temperature of 17.4°C. the immature bird was able to right itself, and at 21.9°C. it cheeped and struggled rather feebly when held in the hand. At body temperatures of 35.5°C. both birds appeared normally active—struggling, squeaking, and "buzzing" their wings.

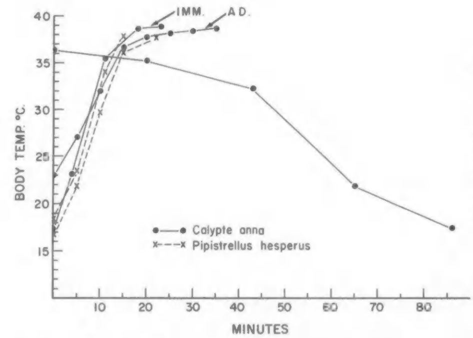

Fig. 6. Rates of arousal from torpor of two Anna Hummingbirds weighing 4.6 and 2.65 gm. and two bats weighing 4.5 and 3.7 gm. The descending curve shows entry into torpor of an immature Anna Hummingbird at an ambient temperature of 2°C.

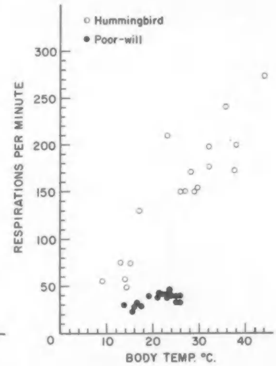

Fig. 7. The relation of body temperature and respiratory rate (excluding periods of apnea) in Anna Hummingbird and Poor-will.

Respiratory rate increased directly with body temperature (fig. 7). At body temperatures below 20°C. respiration tended to be irregular, and at lower body temperatures (9 to 12°C.) periods of cessation of breathing up to five minutes in duration occurred. The maximum respiratory rate of 273 per minute was recorded from an excited bird with a body temperature of 41.9°C. (ambient temperature 22°C.).

Increase in oxygen consumption and body temperature during arousal is strikingly rapid (figs. 5 and 6). The rate of increase in body temperature for the first arousal in each bird was about 1 to 1.5°C. per minute at ambient temperatures of 21 to 23°C. In the adult male, which went through three cycles of torpidity and arousal without food in a 22-hour period, the rate and extent of arousal decreased progressively (fig. 5). Presumably this was due to a progressive decline in the bird's energy reserves. It may be mentioned here that the immature hummingbird consumed one gram of saturated cane sugar solution—almost 38 per cent of its body weight—immediately after arousal from torpor.

We were unable to detect obvious shivering during arousal. Shivering probably occurs but may be obscured by the rapid, deep respiratory movements and the variable quiverings noted in both arousing and fully active hummingbirds.

POOR-WILL

This species, which ranges from central and western North America to central México and which is migratory in the northern part of its range, is the only bird yet known to hibernate under natural conditions (see for example, Jaeger, 1948, 1949, 1954; Brauner, 1952). On November 12, 1955, an adult male Poor-will (*P. n. californicus*) was captured in the Library of the University of California, Los Angeles. According to members of the Library staff, the bird had inhabited the rotunda of the Library at least since November 1, and it had attracted attention by fluttering about in the late afternoons. At the time of capture its weight was 32.0 gm.; as this is less than the weight of any adults recorded by Marshall (1955), it is clear that the bird had not obtained much food. The Poor-will was netted on a high ledge while asleep, and its cloacal temperature within one minute of capture was 39.1°C. These data indicate that the bird, although underweight, was not hiberating.

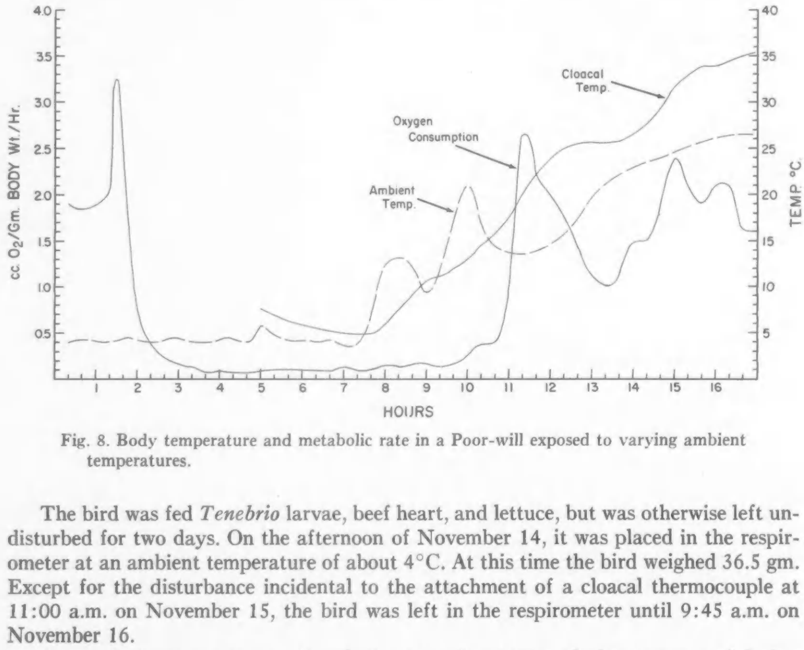

Fig. 8. Body temperature and metabolic rate in a Poor-will exposed to varying ambient temperatures.

The bird was fed *Tenebrio* larvae, beef heart, and lettuce, but was otherwise left undisturbed for two days. On the afternoon of November 14, it was placed in the respirometer at an ambient temperature of about 4°C. At this time the bird weighed 36.5 gm. Except for the disturbance incidental to the attachment of a cloacal thermocouple at 11:00 a.m. on November 15, the bird was left in the respirometer until 9:45 a.m. on November 16.

A record of oxygen consumption during entry into torpor, during torpor, and during arousal, and a record of body temperature during the latter two phases are given in figure 8. Although we have no data on body temperature during entry into torpor, the rapid fall in oxygen consumption (fig. 8) indicates that there was an uninterrupted decline. Body temperature reached a minimum of 4.8°C. and then passively paralleled increasing ambient temperature to 15°C. Body temperature then rose more rapidly than ambient temperature until the bird completed its arousal (fig. 8). Oxygen consumption was extremely low during torpor, but it increased sharply when active arousal began at a body temperature of 15°C.

Respiratory rates in this species are difficult to determine by observation, and for long periods we were unable to detect any respiratory movement although the bird's temperature was increasing. Our limited data (fig. 7) indicate only that the rate varies from 24 to 46 respirations per minute at body temperatures of 13.5 to 26°C.

The posture of the bird during torpidity was exactly as figured by Jaeger (1949:109). No spontaneous movement or changes in position were noted at body temperatures below 15°C. When the bird was handled at a body temperature of 7.5°C., it moved its legs feebly and attempted to elevate its wings but resumed its motionless state when put down. At body temperatures of 15 to 25°C., spontaneous wing-quivering was noted; possibly this was a manifestation of shivering. At body temperatures above 21°C. the side-to-side rocking movement characteristic of Poor-wills was observed. The eyes were kept closed at body temperatures below 22°C. but were usually partly to fully open at higher temperatures. At body temperatures above 32°C. there were quick spontaneous movements as though the bird were alert, and at temperatures of 34 and 35°C. it was able to fly.

During torpidity at the lowest body temperatures, oxygen consumption approximated 0.06 cc./gm./hr. Before torpor the oxygen consumption varied from 1.5 to 3.3 cc./gm./hr., with an average rate of about 2 cc./gm./hr.

PHYSIOLOGY

Torpidity has been reported in a wide variety of birds, but reliable first-hand accounts of this condition are quite rare. There are credible records of torpidity for caprimulgids, swifts, hummingbirds, colies (*Colius*), swallows, and mistletoe birds, *Dicaeum* (McAtee, 1947). However, instances that are documented with data on body temperature or oxygen consumption are known only for the following species: Poor-will (Jaeger, 1949; Thorburg, 1953); Trilling Nighthawk, *Chordeiles acutipennis* (Marshall, 1955); Anna Hummingbird and Allen Hummingbird, *Selasphorus sasin* (Pearson, 1950); Estella Hummingbird, *Oreotrochilus estella* (Pearson, 1953); European Swift (Koskimies, 1948); White-throated Swift, and the Speckled Coly (*Colius striatus*). The last species has been observed in South Africa by Dr. Raymond B. Cowles of the Department of Zoology, University of California at Los Angeles, and he has kindly allowed us to use some of his notes. Cowles found that an individual of this species, when confined in the dark at an ambient temperature of 22°C. for two and one-half hours, experienced a drop in body temperature to 24°C. After one-half hour in the sun, the bird appeared to be fully recovered and had a body temperature of 39.2°C.

In addition to the above instances, a condition of semi-torpor in the Leach Petrel (*Oceanodroma leucorhoa*) has been reported by Folk (1949, 1951).

Temperatures of birds in general are more labile than was formerly realized, but for nearly all species so far studied this lability involves only an increase in body temperature above the usual resting level (38–40°C.). Most adult birds show a negligible decrease in body temperature when subjected to very low environmental temperature (Irving, 1955; Udvardy, 1955). The three species investigated in the present study show a markedly different condition. Normal activity occurs at body temperatures as low as 35°C., and under certain conditions there is a rapid reversible decline in body temperature to 20°C. or more below the usual level.

Entry into torpor.—The physiological factors controlling hypothermia in birds and mammals remain unknown, but there is now sufficient descriptive data to indicate that in birds, as in mammals, this phenomenon is not the same in all species. In contrast to many hibernating mammals (Lyman and Chatfield, 1955:408), birds appear to enter torpor rapidly and uninterruptedly. In swifts and hummingbirds, low environmental

temperatures are not essential for entry into or maintenance of torpidity. Although neurological data are lacking, the abruptness of the decline in body temperature and/or metabolic rate in these species and in the Poor-will suggests central nervous control of the initiation of hypothermia.

In both *Apus* and *Aëronautes,* hypothermia occurred only after considerable loss in weight. There is no evidence at present that hummingbirds must undergo weight loss before becoming torpid. The role of weight loss in the onset of torpidity in caprimulgids is not clear. The three cases in which captive Poor-wills had become torpid all involved birds which had lost considerable weight, but such was not the case with the Trilling Nighthawks reported by Marshall (1955) or the wild Poor-will reported by Jaeger (1949)—the latter bird weighed over 52 grams.

The onset of torpidity in the Anna Hummingbird and Allen Hummingbird, and doubtless other trochilids, is rapid and presumably nightly except in advanced nestlings and incubating females (Pearson, 1950:147; Pearson, 1953:18; Howell and Dawson, 1954).

Neither the experimental procedures of Koskimies (1948) nor our own allowed determination of whether or not a daily period of torpor can occur in adult swifts that have not experienced prior weight loss.

Torpor.—Both the Poor-will and the Anna Hummingbird experienced body temperatures within a few degrees of 0°C. without ill effects, but the White-throated Swifts did not tolerate depression of body temperature below about 20°C. In the three species mentioned above, the capacity for effective behavior improved as body temperature increased. Movements were weak and poorly coordinated at body temperatures below 20°C., well enough coordinated to have survival value between 25 and 30°C., and essentially normal at 35°C.

As active hummingbirds have exceptionally high metabolic rates, it is of interest to compare their oxygen consumption while in torpor with that of a small torpid mammal and that of a small reptile with similar low body temperatures (table 2). The metabolic rates of hummingbirds at body temperatures of 20 to 24°C. are more than twice as high as those of a bat, *Myotis lucifugus* (Hock, 1951), and a lizard, *Sceloporus occidentalis* (Dawson and Bartholomew, 1956) of similar weight at similar body temperatures.

Table 2

Comparison of Metabolic Rates of Small Vertebrates at Low Body Temperatures

Animal	Source	Body temp. Degrees C.	Weight in grams	cc. O_2/gm./hr.
Calypte anna	Present paper	20°	4.3	1.7
	Pearson, 1950	24°	4.3	.8
Selasphorus sasin	Pearson, 1950	22°	3.2	1.24
Sceloporus occidentalis	Dawson and Bartholomew, 1956	20°	4.0	.28
Myotis lucifugus	Hock, 1951	20°	6.2	.39

Arousal.—The rate of arousal from hypothermia is most rapid in the Anna Hummingbird, somewhat less rapid in the White-throated Swift, and much slower in the Poor-will. The first two arouse in a matter of minutes; our observations and those of Marshall (1955) indicate that the Poor-will requires several hours to arouse.

In *Aëronautes,* arousal to normally high body temperatures can occur at environmental temperatures at least down to 4°C.

Since bats and hummingbirds are the only endotherms known to undergo daily cycles

of torpor, a comparison of their rates of increase in body temperature during arousal is of interest. In figure 6, arousal curves of two *Pipistrellus hesperus* of weights approximating those of *Calypte anna* are plotted with comparable data for two Anna Hummingbirds. The curves are strikingly similar. The two species shown are among the smallest of birds and mammals, and we therefore assume that their rates of increase of body temperature are close to the maximum possible.

Oxygen consumption in non-torpid Anna Hummingbird and Poor-will.—Our calculation of the average metabolic rate of a resting non-torpid Poor-will at an ambient temperature of 20°C. is 2.0 cc. 0_2/gm./hr., which is lower than usual for a bird of its size. Unfortunately, there are no other data on metabolism in this species. However, Scholander, Hock, Walters and Irving (1950:264–267) have determined metabolic rates in terms of Calories per day in three individuals of the tropical caprimulgid *Nyctidromus albicollis*. Assuming that one liter of 0_2 consumed by the bird is equivalent to the production of 4.8 Calories, the Poor-will's metabolic rate was 8.06 Calories per day. This is well within the range (7.6 to 13.0 Calories per day) given by Scholander *et al.* for *Nyctidromus*. These authors suggest that the relatively low metabolic rates of their examples of *Nyctidromus* are "probably due to their faculty of hibernation." However, no evidence of hibernation in *Nyctidromus* was obtained, and the authors were merely extrapolating from the case of the Poor-will (Hock, personal communication). As low metabolic rates have been demonstrated in these two species, it may be that other caprimulgids are similar in this respect whether or not they undergo hibernation.

The only published data on the oxygen consumption of hummingbirds are those of Pearson (1950), and our data are consistent with his in those respects which are comparable.

ECOLOGY

Some of the advantages offered to each of the species discussed by its particular pattern of hypothermia have been suggested by the various authors who have published on avian torpidity. Similar suggestions have been made by those who have studied torpor in bats and hibernation in other mammals. We will not attempt to summarize these interpretations but only to add to them where our data permit.

Hummingbirds.—Pearson (1950, 1953, 1954) has pointed out the value of energy conservation through torpidity to these small, rapidly metabolizing birds. A similar interpretation applies to bats, which of course represent an analogous situation in mammals. We would add that the extremely rapid arousal rates (about 1 to 1.5°C./min.) could be advantageous to hummingbirds by reducing the time they are exposed to diurnal predators at sunrise.

Swifts.—The advantages of torpidity to swifts, which are subjected to periods of fasting during unfavorable weather, have been discussed by Koskimies (1948) and Udvardy (1954). Our data show that White-throated Swifts can crawl about at body temperatures as low as 22°C. and can arouse repeatedly even at environmental temperatures as low as 4°C. This means that swifts could move about in their roosts even while hypothermic and that they could arouse and leave in search of food even if the ambient temperature in the roost were near freezing. White-throated Swifts roost in inaccessible locations that are relatively safe from predators, and a more rapid arousal than they showed in the laboratory would not seem to provide any special advantage.

Poor-will.—This species is also an aerial feeder and subject to food shortage during unfavorable weather and cold winters. The advantages to the bird of energy conservation through hibernation are obvious and need not be labored here. It is of interest, however, to use our data on metabolic rates to see how long a torpid Poor-will might survive on its energy reserves. As previously mentioned, our calculation of the metabolic

rate in the resting, non-hibernating Poor-will is about 8 Calories per day. A torpid bird at a body temperature of 10°C. consumed almost exactly one-tenth as much oxygen as the resting bird, giving a value of 0.8 Calories per day while in torpor. One gram of fat when oxidized yields 9.2 Calories; for convenience and conservatism, we will assume that a Poor-will derives only 8 Calories from the oxidation of one gram of its fat. One gram of fat could, therefore, meet the energy needs of a resting bird for one day or of a torpid bird for 10 days. Ten grams of fat could sustain a torpid bird for 100 days, or for even longer if the bird's temperature remained below 10°C. It should be recalled that the weight (52 gm.) of the naturally hibernating Poor-will studied by Jaeger (1949) indicates that an assumed fat deposit of 10 gm. is entirely reasonable.

Arousal rates in the Poor-will seem to be slow and several hours may be required to reach an active body temperature from deep torpor. The Poor-will, however, is protectively colored to an exceptional degree and there is little chance of detection by predators even while the bird is in a torpid or semi-torpid condition. The slow arousal rate, therefore, should offer no particular disadvantage.

SUMMARY

Body temperature and oxygen consumption were measured in captive examples of the White-throated Swift, Anna Hummingbird, and Poor-will subjected to varying conditions of food intake and environmental temperature.

Swifts underwent reduced body temperature and arousal at environmental temperatures of 4°C. and 22°C. but did not recover from body temperatures lower than 20°C. Birds that had lost much weight became torpid more readily than others. The rate of increase in body temperature during arousal was 0.4°C. per minute at external temperatures of both 4°C. and 22°C. Swifts appeared fully active at body temperatures as low as 35°C.

Anna Hummingbirds became torpid at environmental or ambient temperatures from 2°C. to 23°C. A body temperature as low as 8.8°C. was recorded, and metabolic rate during torpor went as low as 0.3 cc. 0_2/gm./hr. Arousal was rapid, with body temperature increasing at the rate of 1 to 1.5°C. per minute at an ambient temperature of 23°C.

A Poor-will became torpid at an ambient temperature of 3.5°C., and body temperature went as low as 4.8°C. Oxygen consumption of the resting, non-torpid Poor-will averaged 2.0 cc./gm./hr., which is relatively low for a bird of this size, and during torpor declined to 0.06 cc./gm./hr. Arousal occurred while the ambient temperature was raised gradually to 22°C. Several hours were required for body temperature to reach 35°C., and the bird appeared fully active at that level.

Arousal rates of hummingbirds and small bats are almost identical, but the metabolic rates of torpid hummingbirds are over twice as high as those of torpid bats or lizards of similar size at similar low body temperatures.

Reduced body temperature and torpor provide a means of energy conservation and are associated with high metabolic rates during activity (hummingbirds) or survival during long periods of fasting (swifts and Poor-will). Calculations show that a torpid Poor-will could survive for at least 100 days on the energy derived from only 10 gm. of fat.

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Department of Zoology, University of California, Los Angeles, California, November 12, 1956.

NATURAL HISTORY OF THE WHITE-TAILED KITE IN SAN DIEGO COUNTY, CALIFORNIA

By JAMES B. DIXON, RALPH E. DIXON, and JAMES E. DIXON

For the past 21 years the White-tailed Kite (*Elanus leucurus*) has been increasing in numbers in northern San Diego County, California, until, in 1956, it has become a common breeding bird. From 1900 to 1935 we had never seen a kite in this area, but since that time we have observed the nesting of kites in 35 different localities. A total of 130 occupied nests has been recorded. The study area comprises the northern half of the coastal slope of the county from the Pacific Ocean to the 1000-foot contour on the western side of the Palomar Mountains.

We wish to express appreciation to the following persons who assisted us in the preparation of this report: Loye Miller, Alden H. Miller, and Jane Durham for suggestions concerning the form and scope of this paper; Oliver P. Pearson for identification of skeletal remains in kite pellets; Bernard Bailey for aid in gathering and dissecting kite pellets; Dale T. Wood for information on a kite roost at Vista, California; and Robert T. Orr for identification of various small mammals trapped. Finally thanks are due our many local friends who helped us in this study.

FOOD

In late February of 1954, Dale T. Wood reported a kite roost in a mature avocado grove of about 10 acres at Vista, California. This orchard (fig. 1) was contour planted at 24-foot intervals. A map was prepared of this roost area on which we plotted 112 places where kites had recently roosted. By raking clear each roosting area in the evening and returning the next morning we could record accurately the number of roosting kites. The fol'owing is a record of these kites and the pellets collected from March, 1954, to January, 1955:

Date	Number of birds roosting	Number of pellets
March 3–4, 1954	39	32
April 1–2	22	30
May 7–8	28	14
June 10–11	10	19
July 6–7	13	31
Aug. 5–6	4	4
Jan. 4–5, 1955	4	4
Totals	120	144

Since pellets of kites are much more compact than those of owls, we feel certain only kite pellets were collected.

A study of the skeletal remains in these 144 pellets reveals that the White-tailed Kite feeds principally on three species of diurnal mice. Meadow mice (*Microtus californicus*) are the most numerous prey, but house mice (*Mus musculus*) and harvest mice (*Reithrodontomys megalotis*) are also taken as well as shrews and other small mammals (table 1). This is in accord with Hawbecker's (1940, 1942) observations which show that *Microtus californicus* is the most numerous food animal.

We have noted that the number of kites present in a given place is directly related to the abundance of food animals in that area. The maximum number of kites has been found in warm, sandy river valleys where there are a few cottonwoods (*Populus fremontii*), black willows (*Salix nigra*), and arroyo willows (*Salix lasiolepis*). Here, in the

open spaces, a dense growth of brome grass (*Bromus rigidus*) and, in damper places, water cress (*Radicula nastertium-aquaticum*) provides a favorable environment for small rodents. Where these areas have been cleared for cultivation or for pasture land, the natural environment for small rodents has been destroyed and the kites have moved into the nearby orchards where, for the most part, the cover crops are mowed and left to lie as mulch. To this the orchardist often adds manure and straw, thus providing an excellent place for meadow mice to breed and in consequence suppling abundant food for the kites.

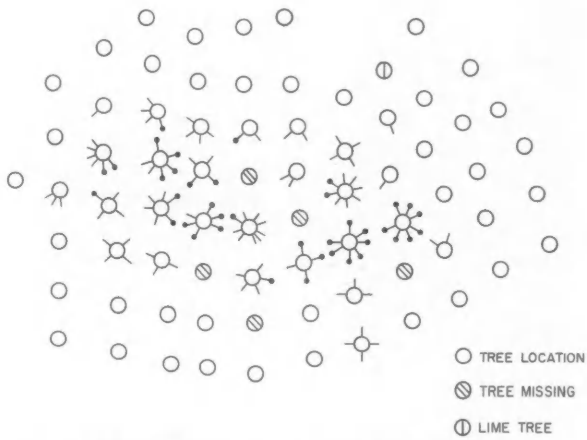

Fig. 1. Schematic diagram of an avacado orchard at Vista, California, used as a roost by White-tailed Kites. Lines extending from trees indicate perches used. Solid dots on lines show locations of 39 kites roosting on the night of March 3, 1954.

Table 1

Skeletal Remains in Kite Pellets from Roost near Vista, California

Date	Number of pellets	Meadow mice	House mice	Harvest mice	Other contents*
March 1–4, 1954	32	33	4	2	4
April 1	20	31	12	2	0
May 7	14	14	1	0	2
June 10	19	18	9	1	0
July 6	31	22	10	6	1
Aug. 5	14	15	2	1	0
Jan, 4, 1955	4	1	4	1	0
Totals	144	134	48	13	7
Percentages		66	24	6½	3½

Average number of items per pellet—1.4.

* 1 deer mouse (*Peromyscus maniculatus*), 1 shrew (*Sorex* ?), 1 gopher (*Thomomys* ?), 1 wood rat (*Neotoma* ?), 1 unidentified small mouse, two small birds. There were no insect remains.

In one valencia orange orchard where an unusually heavy cover crop had been plowed under and which had been mulched with 80 tons of race track straw, there occurred a heavy infestation of meadow mice. This orchard was a favorite feeding ground for kites in the fall of 1953 and the spring of 1954 and three pairs nested in nearby orchards. Two of these pairs had nests in orange trees and the third pair nested in a large avocado tree. All three pairs reared their young successfully and were seen in the area until the latter part of July. In the spring of 1955 this orchard was again visited by kites. However, the trees had suffered such heavy rodent damage that the orchardist had adopted a method of "clean cultivation" to get rid of the mice and as a result the kites soon left for other feeding areas.

In late May of 1940, we observed kites gathering in large numbers in a river bottom area. Here we noted 34 kites roosting in a dense growth of willows and cottonwoods only a few miles from the ocean. The kites remained in this area several weeks and hunted along a sewer drain where the heavily nitrogenized water had stimulated a luxuriant growth of water cress. A high population of meadow mice was present in this lush vegetation, providing an excellent feeding ground for the kites.

In this group of birds we noted a large percentage of young and also some indication of family groups. We feel reasonably sure that this flock contained offspring of kites which had nested nearby. There were three occupied kite nests in one grove of trees within a radius of 500 feet and in adjoining groves we saw two more breeding pairs.

The abundance of both kites and owls in the study area rises and falls with the increase or decrease in numbers of rodents. The sizes of the small rodent population in coastal San Diego County suggest a seven-year cycle. In the years of high populations (1943 and 1950) more breeding kites were found and we think they were prone then to lay more eggs per clutch. In periods of plentiful food supply, pairs often attempted two broods in one season. Our observations suggest that if ample food is present, an area of about 20 acres of mouse pasture is large enough to support a pair of nesting kites and their brood.

In partial support of the hypothesis that an abundant rodent population is the governing factor in the breeding of the White-tailed Kite we offer the following: three different localities, where one might expect to find a high population of mice, were picked at random from our field note records and searched for kites. In each place we found a breeding pair.

The Red-shouldered Hawk (*Buteo lineatus*) is able to maintain itself in areas abandoned by kites. Perhaps this is possible because the hawk is not as restricted as the kite in its diet; it feeds not only on mice, but also on snakes, frogs, lizards, small rabbits, and squirrels. Both the kite and this hawk have increased in numbers in the study area although there has been a large increase in human population. We think that these raptors will continue to increase as long as the prey upon which they depend is available. Both species seem able to adapt themselves to changing conditions as long as their food supply is not eliminated.

NESTING

The first indication of the onset of the breeding season is the presence of a single kite sitting on a desirable perch in the top of a tree or bush. Thereafter the bird may be seen in that place at certain hours of the day with surprising regularity. The earliest date we have noted this has been November 10 and the latest date March 10. Soon after the first bird has been sighted a second kite makes its appearance and the two birds hunt together.

Breeding starts with attempts of the male to copulate. These first attempts are in-

variably repulsed by the female (Hawbecker, 1942). The male then, in many instances, endeavors to select a nesting location and even makes a haphazard effort at nest building. The site he chooses is apparently not acceptable to the female, for we have never seen a female use such a nest site when she started building.

Fig. 2. Typical kite feeding area. Note overgrazing in foreground and dense grass beyond fence. Dead willows behind were used as perches.

Nesting sites.—Kites nest in any suitable tree of moderate height. We have found them using the following introduced trees: pepper (*Schimus molle*), avocado (*Persea gratissima*), orange (*Citrus sinensis*), eucalyptus (*Eucalyptus masculata*), and olive (*Olea europaea*). We have also found kites nesting in the following native trees: cottonwood (*Populus fremontii*), black willow (*Salix nigra*), live oak (*Quercus agrifolia*), sycamore (*Platanus racemosa*), and toyon (*Photinia arbutifolia*). Pickwell (1930) lists a number of kinds of nesting trees compiled from records in the literature, and Hawbecker (1942) states that any suitable tree may be used for nesting that is near the required food source.

The earliest nesting date (two eggs in nest) we have recorded is February 6 and the latest is July 10 (4 eggs in nest). Twice we have found young kites at least 10 days old on February 22 which would indicate laying earlier than February 6.

Nest building.—With the beginning of actual copulation the female selects a nesting site and starts to build. Some authors (Hawbecker, 1942; Watson, 1940) state that both sexes work on the nest, but our observations indicate that nest building is done almost entirely by the female.

Hawbecker (*op. cit.*) records a nest completed in seven days, but we found that

construction of the nest takes from 14 to 28 days. The male sometimes accompanies the female on her nest-building flights and upon rare occasions brings back nest material. If this occurs, the material is taken by the female and arranged to her satisfaction. In securing the hard, dry twigs for the outer part of the nest the female does not pick them off the ground but breaks them from standing trees or bushes with her bill. She then carries them to the nest in her bill. Sometimes these twigs are difficult to obtain and the female may perform odd maneuvers in acquiring them.

When viewed from the outside, the nest appears flimsy, but a closer inspection of the structure indicates that it is strong and well designed. Pickwell (1930:224) calls the nest a "loose pile of dry sticks," but Bent (1937), Hawbecker (1942), and Watson (1940) report that the nest is well built. The nest may be lined with straw, grass, or rootlets (Pickwell, *op. cit.*). In our study area the hard, dry roots of salt grass (*Distichlis spicata*) or Bermuda grass (*Cynodon dactylon*) are preferred, but if these are not available, the dry, hard stems of last year's wild oats are used.

The measurements of a typical nest are as follows: outside diameter 21 inches, depth 8 inches; inside diameter 7 inches, depth 3½ inches.

Kites do not use the same nest over and over; they always seem to build new ones. Only two nests observed were built on top of old nests of other birds. A nest of a Cooper Hawk (*Accipiter cooperii*) was used as a foundation in one instance and a crow nest in another. All other nests seen were constructed entirely by the kites.

"Flitterflight" of male.—In the nest-building period and quite often after the female kite is incubating the eggs, we have observed the male kite flying in a peculiar manner. We have called this the "flitterflight." Watson (1940) calls it the "quiverflight." In this flight the male leaves his customary perch and proceeds to fly around and around over the nesting grove. He holds his wings in a V-shape directly overhead and rapidly vibrates them at the same time making a chittering sound. After circling the grove several times the kite returns to its perch and rests there for a considerable period before going forth to hunt again. This very odd flight can be seen from some distance and it has been the means of our locating many nests we might otherwise have overlooked in the dense growth of river bottoms.

Territoriality.—We noted no territorial fighting among the kites. They seem to be more sociable than other raptorial birds, although Watson (1940) reports definite territoriality among the kites he studied.

Protection of nest.—In the course of nest building the female stands constant guard over the nesting area. She will attack savagely any of the large raptorial birds that come near her perch. The male sometimes joins in these attacks and we have seen the pair haze Golden Eagles (*Aquila chrysaëtos*), Red-tailed Hawks (*Buteo jamaicensis*), and Red-shouldered Hawks. Such protective action has been reported by Moore and Barr (1941) and by Hawbecker (1940). Kites seem able to stay above the larger birds and can inflict enough damage to cause the intruders to leave the area hurriedly. However, Turkey Vultures (*Cathartes aura*), Marsh Hawks (*Circus cyaneus*), and Cooper Hawks were never attacked.

Relations with Crows.—We witnessed only two instances where Crows (*Corvus brachyrhynchos*) destroyed the eggs of the kite and only one instance of crows mobbing to death a young kite just out of the nest.

Crows scavenge from the kites at every opportunity and use every means to get food away from them. We have seen a crow alight on the same limb with a feeding kite and proceed to crowd sideways into the kite to make it drop its food. The other kite of the pair was perched within a few feet and while it watched with interest it made no effort to intercede.

Table 2

Eggs and Young of White-tailed Kite at Twenty-three Nests

Date	Number of eggs laid	Number of young leaving nest	Number of young banded
June 13, 1937	5	3	3*
April 14, 1940	4	4	2
April 5, 1942	4	4	4
May 16, 1942	4	2	2
May 17, 1942	3	2	1
April 18, 1943	4	2	2
May 2, 1943	4	3	2
May 4, 1944	4	2	2
May 4, 1944	4	4	4
May 4, 1944	4	4	1
May 8, 1944	4	4	4
May 22, 1944	4	3	3
May 27, 1944	4	4	4
May 27, 1944	4	3	1
April 28, 1946	4	3	3
April 28, 1946	4	4	4
June 23, 1946	4	4	4*
April 27, 1947	4	4	4
April 27, 1947	4	3	3
April 27, 1947	4	3	3
March 16, 1950	6	4	4
April 18, 1950	4	2	2
April 28, 1950	4	3	3
Totals	94	74**	65

* Second nesting for season. ** Nine young escaped without bands.

EGG-LAYING AND INCUBATION

Hawbecker (1942) estimates the incubation period as 30 to 32 days, but we have never established an accurate incubation period because the egg-laying period is rather prolonged. In addition, most of the nests are inaccessible. We regularly checked nest contents with the aid of a mirror mounted on a long pole, but only 23 nests were so situated as to allow banding of the young kites (table 2). Of the 124 nests checked, one contained six eggs, 15 had five eggs, 106 had four eggs, and two had three eggs. Eight of the 15 nests containing five eggs were found in one season of high mouse population (1950).

Eggs vary in coloration even within a single clutch. One cannot follow the nesting of a female season after season by the appearance of her eggs as is possible in many other raptorial birds. Eggs vary from pure white to a heavily marked condition in which there are light purple and rust-red spots and blotches. These vivid colors fade during the incubation period. Hawbecker (1942) states that the eggs he observed were chocolate brown when first laid but that they soon faded to mottled brown and tan.

Differing from most raptorial birds, the female kite does all the incubating of the eggs. She leaves the nest at this time only for short periods to stretch and to preen her feathers. Hawbecker (1942) and Watson (1940) have likewise observed that the female alone incubates the eggs.

YOUNG

Young kites when newly hatched are covered with a grayish down quite different in color from that of other raptorial birds which nest in this area (fig. 3). Hawbecker

(1940) agrees with our observation that at first there is a variation in the size of the young. However, by proper feeding the female closes this "gap," for there is never over two days' time between the dates of leaving the nest by the oldest and youngest birds.

The female appears to do all the feeding of the young and she is very careful to give each bird its proper quantity of food. When the young grow older and show some signs of hoggishness, she wards off an aggressive bird by striking it between the eyes with the elbow of her wing. This treatment seems to be very effective.

Moore and Barr (1941) have described the plumage of the young kite. We have observed that when the young birds leave the nest (fig. 4) they are quite different in

Fig. 3. Nest and eggs of White-tailed Kite.

appearance from their parents, having a number of reddish feathers on the breast and in shoulder patches. This reddish plumage and their ungainly flight enabled us to distinguish young from the parents as long as they were in a family group.

We agree with Hawbecker (1942) that after the young leave the nest they return there at night to roost, and they often return in the daytime to eat. The nest is a sanctuary from various birds of prey. We have noted that the percentage of young leaving the nest is large and this coupled with the habit of raising two broods may account for the rapid increase of kites in the study area.

The parents "wean" the young by flying into them roughly and driving them from the nesting area. The young are not permitted to return. From a nest that held a complete clutch of eggs on March 10, weaning took place on July 15. In this area the following season weaning took place on July 17.

Banding.—The time when the young can be secured for banding is very short. From four to six weeks of age is the best time. If older than six weeks, the young swarm out of the nest, even when it is approached on the ground. They cannot fly far at this

age, but they are difficult to catch. Sometimes when the young are being banded the parent birds try to defend them by diving down and lightly striking the climber and scolding with a rasping note which is more like that of a falcon than that of a hawk.

Of the broods banded, 15 were located in cottonwood trees, five in live oak, two in orange trees, and one in a black willow. To date we have received only three returns of bands. They are as follows: one young kite, banded on May 16, 1943, was found dead on January 26, 1944, about 12 miles east of the point of banding; one banded on May 4, 1944, was found dead under the nest tree on May 30, 1944; and one banded on April 28, 1946, was killed on November 11, 1948, about 100 miles north of the point of banding.

Fig. 4. White-tailed Kite at nest with small young in cottonwood tree.

Second nestings.—The male tries to stimulate the female to undertake a second nesting for the season. This is done by nest location search, by repeated copulations, and by abortive nest constructing attempts. There are several instances on record where the female started a second nest before the young had left the first nest.

HUNTING

From the time the female chooses the nest site until the young leave the nest the male does all the hunting (Watson, 1940). The female sits on her perch, occasionally nest building and awaiting the arrival of the male with food. When the male arrives with food, she flies to meet him if she is hungry and she will take the food from his claws in midair. If the female refuses food brought in by the male, he eats it himself or stores it in a nearby tree. These food storage places are usually in a shallow hollow in a large limb of a tree or in a split limb where food can be wedged in until needed.

The male kite is a very good hunter. We once timed a hunting male and found that he caught three mice and delivered them in eight minutes. The first mouse went to a young bird, the second was taken by his mate, and the third he ate. These three mice were caught in a two-acre tract of land that was tightly fenced and heavily covered with

needle grass (*Bromus rigidus*). Here the grass had accumulated over the seasons until a mulch several inches deep had covered the area. In this place we also noted a female coyote (*Canis latrans*) lying flat on her stomach with one paw raised. Soon there was a wriggling in the dry grass in front of her and she brought her paw down quickly but firmly and reached under it with her nose and withdrew a meadow mouse. This locality contained the greatest concentration of meadow mice we observed. The surrounding area was somewhat overgrazed and this no doubt had forced the mice into this area.

Fig. 5. Young White-tailed Kite just out of nest.

When hunting, the kite flies rather low and usually not more than 200 feet above the ground. Flying into the prevailing wind, it hunts until it sees something of interest whereupon it stops and takes a stationary stance by slowly flapping its wings. Usually a kite will follow its prey for some time, dropping down nearer to the ground and again taking up the stationary stance. When it is finally satisfied that the prey is in a catchable situation, it folds its wings in a steep "V" overhead and drops vertically on the prey. Being equipped with needle-like talons the kite seems very successful in striking the prey through dry cover.

ROOST ACTIVITIES

We have already described a roosting concentration that may involve as many as 39 individuals in the non-breeding period. On the evening of March 6, 1954, we made the following observations in this roosting area (fig. 1) at Vista, California. At 5:35 p.m.

the first kite appeared and, after hunting unsuccessfully in the vicinity, it went to roost. From 5:35 to 6:12 p.m. we watched 22 kites arrive and go to roost. At 6:30 p.m. we took up an observation point within 300 feet of the roosting birds in a place where we would not disturb them. Here we noted a few stragglers still coming in to roost; they seemed to come from all directions and they did not fly around before going to roost as the earlier arrivals had. Alighting on the highest points on the trees, they faced into the prevailing wind and apparently settled for the night.

The owner of the ranch immediately west of the roosting area reported that there had been a gradual building up of the number of roosting birds for three seasons. He also said that they were early risers, as most of them were gone by 6 a.m. Few of the individuals here showed any indications of the reddish breast plumage or ungainly flight patterns of young birds. Apparently many of these birds drifted away to breeding areas in the spring and summer of 1954.

Morgan (1948) reported a kite roost near Camp Pendleton, Oceanside, California, where as many as 25 kites were seen at one time.

SUMMARY

The White-tailed Kite is now a common breeding bird in the northern half of coastal San Diego County, California. Nesting of kites has been observed in 35 localities in this county and 130 occupied nests have been recorded.

A study of 144 kite pellets reveals that meadow mice (*Microtus californicus*) are the principal prey. The maximum number of kites are to be found in areas where there are large concentrations of meadow mice.

Nesting dates extend from early February to July 10. The female does most of the nest building and all the incubating of the eggs. The majority of nests examined contained four eggs, but eight nests noted with five eggs were found in one season of high mouse population (1950).

In 23 nests closely watched 94 eggs were laid and 74 young survived to leave the nest.

The male kite obtains all the food for the incubating female and the young. Food may be stored in small caches in trees. Crows repeatedly scavenge food from kites and may destroy eggs and young.

Roosting concentrations of non-breeding birds may occur in which as many as 39 kites assemble in a small area.

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Escondido, California, September 1, 1956.

THE EVOLUTIONARY AND TAXONOMIC SIGNIFICANCE OF SEXUAL DIMORPHISM AND HYBRIDIZATION IN BIRDS

By CHARLES G. SIBLEY

INTRODUCTION

Some of the most difficult problems in avian systematics concern the generic level of classification in groups with a high degree of sexual dimorphism. The hummingbirds, manakins, birds of paradise, pond ducks, grouse and pheasants provide examples. In all of these groups there are two lines of evidence which provide indications of relationship, but which, frequently, appear to conflict with one another. On the one hand the male plumage characters of related species are highly diverse and, judged on a "degree of difference" basis, argue for wide taxonomic separation. At the same time the female plumages may be very similar. Viable, often fertile, hybrids may result from interbreeding between species with extremely different looking males.

When the taxonomist attempts to evaluate these various pieces of evidence he is faced with the decision as to the proper emphasis to be accorded to each. Which is more important: the secondary sexual characters of the males, which seem to argue for the separation of certain species into different genera, or the similar females and viable hybrids which seem to indicate a closer degree of relationship? Most taxonomists have tended to search for, and to emphasize, differences. The result has usually been that the characters of the diverse males have been utilized as the principal criteria while the similarities among the females, and the evidence from hybrids, have often been ignored. In all of the groups previously mentioned this has led to a high degree of generic splitting and has resulted in an inordinately large proportion of monotypic genera. Within the past few years, due mainly to the work of Ernst Mayr and Jean Delacour, this situation has been largely remedied in the ducks, pheasants, and birds of paradise, but the other groups still bear an excessive burden of generic names in current usage. Many avian taxonomists will agree that some groups of birds are overly split generically, but even a widely held opinion is insufficient grounds upon which to advocate or undertake the extensive revisions of hummingbird genera, for example, which some believe are needed (see Van Tyne, 1945).

The first requirement is a conceptual basis upon which to evaluate the taxonomic significance of sexual dimorphism and hybridization. To arrive at this in turn requires an understanding of the origin and function of the characters used in taxonomy and of the selective forces which determine their evolution. The reasons for, and results of, interspecific hybridization must be understood before its significance in systematics will be clarified.

It is the purpose of the present paper to review the process of speciation, especially as it pertains to the evolution of secondary sexual characters; to consider the results of secondary contacts which permit hybridization; to establish the relationship between different pair-bond patterns and the degree of sexual dimorphism, and to relate these various subjects to one another and to the taxonomy of certain groups of birds.

THE PROCESS OF SPECIES FORMATION

It is generally agreed that the process of speciation, at least in most animals, is accomplished through the interaction of heritable variation, natural selection, and spatial isolation. The first step in the process is the splitting of a single, interbreeding population into two spatially isolated populations. Since mutation, recombination and selection will be different in each of these daughter populations, they will diverge genetically from

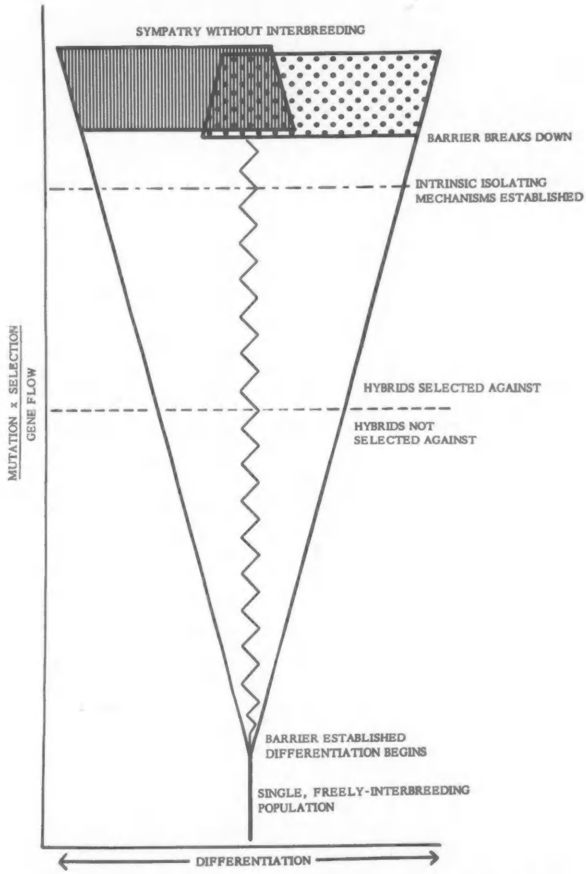

Fig. 1. Diagram of the process of speciation according to Muller.

each other and from their common ancestral type. Muller (1939, 1942) has postulated that the gradual accumulation of genetic differences in such isolated populations eventually results in the establishment of intrinsic isolating mechanisms which prevent interbreeding if the extrinsic barrier breaks down. Figure 1 diagrams the process of speciation according to Muller's hypothesis.

Since speciation is gradual there exists the possibility that the extrinsic barrier may break down before intrinsic isolating mechanisms have become fully effective. If this occurs the two partially differentiated populations are presented with the opportunity to interbreed. The extent and results of such hybridization will largely depend upon the degree to which they have diverged genetically during the period of spatial isolation.

In the present paper the term "hybridization" will be used to indicate interbreeding between populations in secondary contact regardless of their taxonomic rank. Mayr

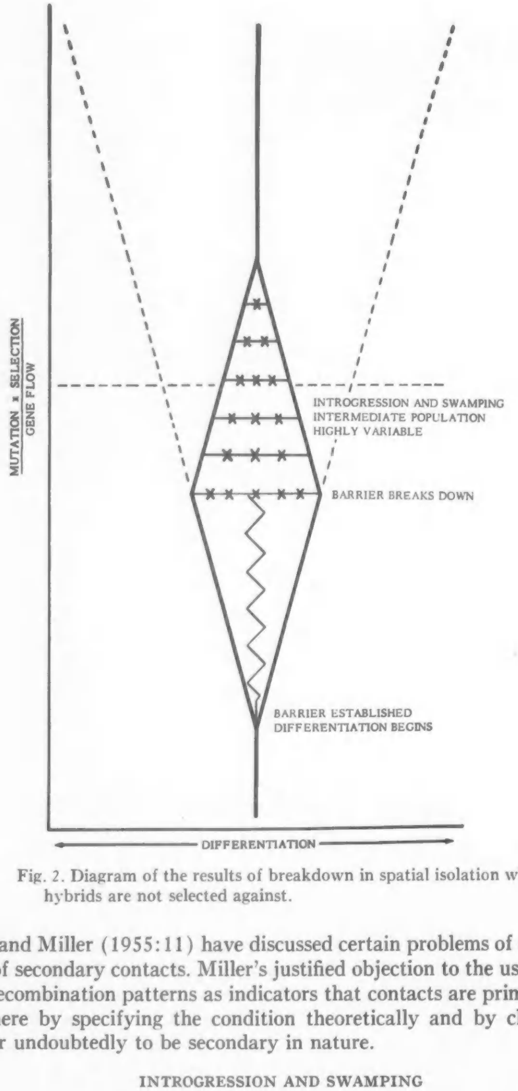

Fig. 2. Diagram of the results of breakdown in spatial isolation when hybrids are not selected against.

(1942:258) and Miller (1955:11) have discussed certain problems of definition and the recognition of secondary contacts. Miller's justified objection to the use of hybrid segregation and recombination patterns as indicators that contacts are primary or secondary is avoided here by specifying the condition theoretically and by choosing examples which appear undoubtedly to be secondary in nature.

INTROGRESSION AND SWAMPING

If the extrinsic barrier between diverging populations breaks down before marked ecological, morphological or physiological differences have accumulated, the hybrid individuals resulting may be fully fertile and viable. If they have as high a reproductive potential as the parental types they will be at no selective disadvantage in comparison with the parents and will form a bridge between the parental gene pools. For a time this

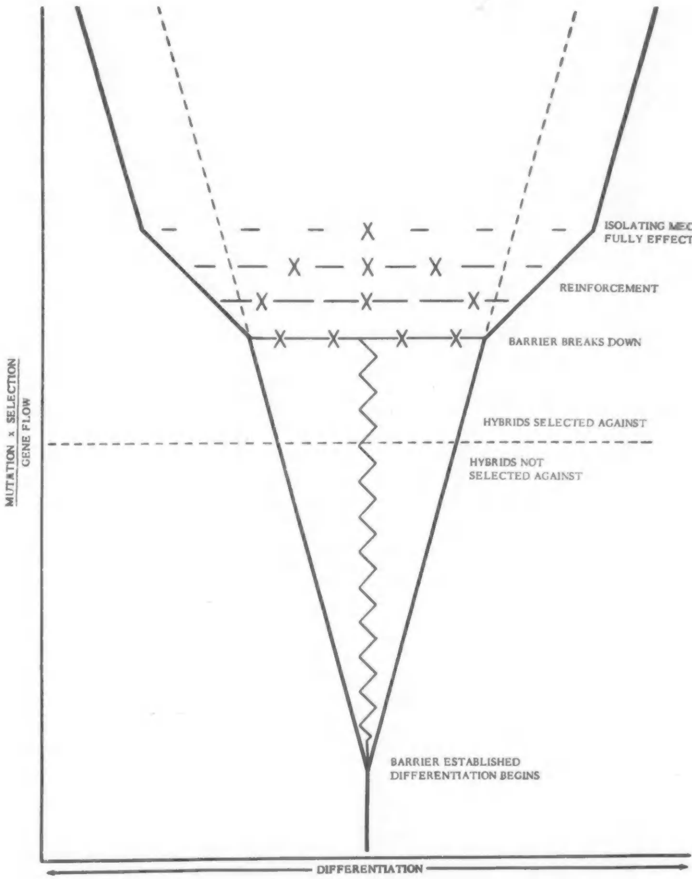

Fig. 3. Diagram of the results of breakdown in spatial isolation when hybrids are selected against.

will result in an increase in the variability of the rejoined populations due to the new recombinants present. As selection fashions a new adaptive peak the variability will decrease to a normal amount. Figure 2 diagrams this situation.

HYBRIDS SELECTED AGAINST—REINFORCEMENT

If, on the other hand, by the time the extrinsic barrier fails, sufficient differences have accumulated to render the hybrids less fertile or less viable than the pure parental individuals, a source of selection against the individuals entering into hybridization has been attained.

This hypothesis was first proposed by Fisher (1930), further discussed by Sturtevant (1938) and elaborated by Dobzhansky (1940). As described by Dobzhansky

(1951:208), "This hypothesis, which is complementary to Muller's, starts from the same premise, namely that the genotype of a species is an integrated system adapted to the ecological niche in which the species lives. Gene recombination in the offspring of species hybrids may lead to formation of discordant gene patterns. This decreases the reproductive potentials of both interbreeding species." The result is that the individuals in each parental population which enter into hybridization produce fewer offspring than those which do not. Thus the genotypes of the non-hybridizing individuals are at a selective advantage. The genetic basis for the better isolating mechanisms thereby increases its frequency, and any mutation which provides an additional basis for interspecific sexual isolation will be selected for. Through this process the isolating mechanisms of each of the participating populations will be reinforced relative to the other until gene exchange between them is virtually or entirely stopped. Figure 3 illustrates this hypothesis.

A convincing proof of this idea has been provided by Koopman (1950) utilizing *Drosophila pseudoobscura* and *D. persimilis* in a population cage experiment. Interspecific matings were selected against by eliminating all hybrids in each generation. In one series the percentage of hybrids dropped from nearly 50 per cent in the first generation to one per cent in the fourth generation and, except for single generation fluctuations, remained below three per cent for the remaining eight generations of the experiment.

Further, but less direct, evidence that selection against hybrids can reinforce isolating mechanisms has been provided by Dobzhansky and Koller (1939) in their study of sexual isolation between *Drosophila pseudoobscura* and *Drosophila miranda*. Strains of the two species from areas of sympatry, or near sympatry, show greater sexual isolation than those from areas far removed from the region of overlap. Similarly King (1947) found that sexual isolation between the two sympatric Brazilian species, *Drosophila guarani* and *D. guaru*, was much better than between either of the Brazilian species and *D. subbadia* of México. Huxley (1940:15) has also commented on this point.

Additional examples and a discussion of the genetics of isolating mechanisms have been provided by Dobzhansky (1951), who summarizes (pp. 210–211) as follows: "It is important to remember that the formation of reproductive isolation . . . requires time. The first vestige of the isolation develops . . . in allopatric populations. Inviability of F_1 hybrids, and low average adaptedness of the F_2 and of backcross products are probably by-products of the genetic differentiation of allopatric populations. Here the mechanism suggested by Muller is probably most important. The hybrid inviability and breakdown provide, then, the stimulus for natural selection to build up other reproductive isolating mechanisms. Reproductive isolation diminishes the frequency of the appearance of hybrids, prevents the reproductive wastage, permits the populations of the incipient species gradually to invade each other's territories, and finally to become partly and wholly sympatric. It is during the latter stages of this process that the selection pressure bolstering the reproductive isolation becomes strongest, helping to complete the process of speciation."

INTERMEDIATE SITUATIONS

Between the extremes of swamping when hybrids are not selected against and reinforcement of isolating mechanisms when hybrids are selected against, there exist situations in which selection is neutral or in which the hybrids are able to thrive in an ecological situation intermediate between those required by the parental types.

An interesting example is found in the narrow hybrid zone which exists between the European Hooded Crow, *Corvus cornix*, and the Carrion Crow, *C. corone* (Meise, 1928).

The width of this hybrid zone "is from 75 to 100 kilometers, and there is no evidence that it has broadened materially within the last 5,000 years" (Mayr, 1942:265–266). In this situation the isolating mechanisms have not become reinforced to the point of preventing hybridization nor has introgression caused swamping. Apparently alien genes are selected against in each of the parental populations but the hybrids are favored in the ecologically intermediate area. Some evidence for this explanation comes from the facts that with the well-known climatic shift occurring in the northern hemisphere the two species of crows are shifting their ranges and that the hybrid zone, although maintaining its width, is shifting in accordance.

ISOLATING MECHANISMS

The useful term "isolating mechanism" was proposed by Dobzhansky (1937) to describe agents which curtail or prevent gene exchange between populations. Classifications of isolating mechanisms have been proposed by several authors (see Dobzhansky, 1951:181–182; Stebbins, 1950, chapt. XI).

The nature of the isolating mechanisms which evolve will depend upon the means by which the organisms involved achieve recognition and/or fertilization. In wind-pollinated plants gametic incompatability or hybrid sterility are possible mechanisms. Insect-pollinated plants may utilize the visual and olfactory senses of the insect pollinators as isolating mechanisms as Mather (1947) found in *Antirrhinum*. Some insects have evolved isolating mechanisms dependent upon chemoreceptors (probably olfaction) as determined by Miller (1950) in his study of *Drosophila affinis* and *D. algonquin*. Mayr (1950) found that sexual isolation between *D. pseudoobscura* and *D. persimilis* depends upon olfactory stimuli received via the antennae of the females. Removal of the antennae of the females greatly reduces sexual isolation between these species. Spieth (1952) has studied a large number of species of *Drosophila* to determine the species-specific differences in mating behavior which function as isolating mechanisms. The subgenus *Drosophila* utilizes contact stimuli while members of the subgenus *Sophophora* have developed signals such as movements and olfaction which function without physical contact.

Crane (1941) studied the behavior of fiddler-crabs (*Uca*) in Panamá. The males of each of the twenty-seven species present have a species-specific pattern of claw structure and display movement which function to warn off other males and to attract females of the same species. In spiders (Kaston, 1936), recognition is by sight in some groups, by both visual and tactile stimuli in others, and by touch alone in still others. Frogs and toads utilize species-specific vocal calls, pre-amplectic behavior patterns, and reactions during amplexus as isolating mechanisms (Jameson, 1955). Nocturnal mammals apparently utilize olfaction and hearing in species recognition; diurnal species depend more upon vision and less upon hearing and scent. Further examples are given by Dobzhansky (1951, chapt. VII).

In birds the senses of vision and hearing are especially acute while the sense of smell is totally or nearly absent in most birds. Diurnal species possess ranges of color vision and hearing similar to those of man. It is therefore to be expected that isolating mechanisms in birds will be primarily dependent upon visible and auditory characters in the form of colors, structures, display movements, and sounds. These signal characters function as "releasers" (Lorenz, 1935, 1937; Tinbergen, 1948, 1951) which activate innate patterns of response in other individuals, usually of the same species. The signal characters which function in species recognition and in pair formation are most important as isolating mechanisms. It is these which will be reinforced by selection against hybrids in a secondary contact.

Before signal characters can be fully utilized in taxonomy, it is necessary to determine their *function* and, for display movements and sounds, their *motivation* or drive, or "the complex of internal and external states and stimuli leading to a given behaviour" (Thorpe, 1951, 1954). Behavior patterns which function as interspecific isolating mechanisms will have a different taxonomic significance from those which function as signal characters in intraspecific responses. Furthermore, there are many stereotyped, innate behavior patterns connected with comfort movements such as scratching, preening, and stretching or with feeding behavior or sleeping postures which have phylogenetic significance at the familial or ordinal level (Heinroth, 1930). A behavior pattern called "courtship" may actually function both as an isolating mechanism and also as a hostile display. It may have been derived from a completely hostile pattern and be motivated by internal drives of escape, attack, and sex in varying relative and actual intensities. The isolating mechanism component may be of taxonomic value at the species level while the hostile component may have generic value. In their excellent revision of the ducks (Anatidae), Delacour and Mayr (1945), believing that genera should reflect similarities, were more impressed by the similarities between species in "courtship" patterns than by the differences which also exist. It seems logical to expect that the hostile components will be similar in a group of species like the anatine ducks while the isolating mechanism components will be specific and hence dissimilar in sympatric species. By using the similar components, which probably function in hostile responses between as well as within species, Delacour and Mayr found the "courtship" behavior patterns to be of generic significance.

The discussions of ethological isolating mechanisms by Mayr (1942:254), Lack (1945:62) and Huxley (1938, 1940) are of interest. Marler (in press) has investigated the taxonomic value of certain signal characters.

INTERSPECIFIC RESPONSES

There is another point which is significant in organisms having ethological isolating mechanisms. Hybridization is the proof that members of different populations have interbred and, as noted, if selection is against the hybrids, isolating mechanisms are reinforced. However, any expenditure of time, energy or gametes which fails to produce offspring will be selected against and will contribute to the reinforcement of isolating mechanisms. Hybridization should therefore be looked upon as the proof that interspecific pairing responses have occurred, but lack of hybridization does not prove that such responses are absent. In birds, which use vision and hearing in species recognition, it is apparently this source of selection which has been important in producing diversity in visible and/or audible characters among sympatric species. Such selection is effective between any two species which interact, regardless of their phylogenetic relationship. If, for example, individuals of two unrelated species are mutually attracted to one another for even a short period they will reduce their chances of successful breeding with members of their own kind. Presumably they were so attracted because of imperfections in their isolating mechanisms, hence any reduction of their reproductive success increases the incidence of those genotypes with the better isolating mechanisms.

This type of selection becomes especially intense when the length of time during which the members of a pair are associated before copulation occurs is very short. A short pair bond places a greater premium upon rapid and correct species recognition. Selection against errors in recognition will act to reinforce the characters used in recognition. Such characters are, by definition, isolating mechanisms.

SEXUAL DIMORPHISM

To this point the discussion has been sufficiently general to apply to most or all groups of animals. Our principal concern, however, is with the generic concept in those groups of birds having a high degree of sexual dimorphism.

In the foregoing discussion of hybridization evidence has been presented which indicates that the degrees of difference in the isolating mechanisms of sympatric species may be increased if selection is against interspecific responses pertaining to pair formation. This, obviously, can function only if two or more interacting species are in contact. A second source of selection, tending to increase the degree of difference between the sexes of a species, is derived from the competition among individuals for mates. This selective pressure is independent of the presence of other species, hence is always present. It is this source of selection which has long been known as "sexual selection."

The theory of sexual selection was proposed by Darwin (1871) to explain the origin of such secondary sexual characters as the bright colors, displays and songs of male birds, the antlers of male deer and similar structures which result in sexual dimorphism. Sexual selection was conceived by Darwin as resulting from the competition among males for mates, hence any heritable variation which gave an individual male an advantage in securing mates would increase in frequency in succeeding generations. Darwin's theory fell into disrepute for a period because it seemed to require a conscious ability on the part of female animals to discriminate among the small degrees of individual variation in the males. With the better understanding of instinctive behavior, which has accompanied the relatively recent rise of the science of ethology, it has become apparent that this objection is specious. With but slight modification in wording Darwin's concept may be shown to apply with special significance to certain groups of animals and to be of great importance in several families of birds.

In most birds it is the males which possess the species-specific colors, structures, sounds or displays ("releasers") which function as the basis for instinctive species recognition. Females, presumably, possess an innate perceptory pattern ("innate releasing mechanism") which matches and responds to the signal characters of the male. Pairing responses of the female depend upon the encountering of the male when her physiological thresholds are at certain levels. In species which are monogamous, or which pair for life, there will be but limited competition among males for mates. However, in polygamous species with a short pair bond a higher selective premium is placed upon any character in the male which more strongly stimulates the instinctive pairing responses of the females. It is this which Darwin called sexual selection, and it may be defined as *the reproductive advantage accruing to those genotypes which provide the stronger heterosexual stimuli.* It seems certain that the intensity of this source of selection reaches its maximum in those species in which several males gather to display on a "lek," or "booming ground," to which the females come for fertilization. In such species the pair bond lasts only for the period of copulation and an individual female has a "choice" of several males.

The result of sexual selection is sexual dimorphism. In species utilizing vision in recognition it will be visible characters which are affected. The genetic basis for such characters may, and probably does, involve but a very few genes and these may control only relatively superficial characters of plumage and display movements. This seems to explain why species with very different looking males and similar females can produce viable, often fertile, hybrids. The complete process appears to be as follows.

In polygamous species sexual selection produces high degrees of sexual dimorphism by action upon a few genetic factors in the males. When such species become separated into geographically isolated populations the secondary sexual characters of the males,

in each population, evolve more rapidly than other characters. Because available mutations will, by chance alone, be different in these separate populations, the males of the two groups come to look and/or sound extremely different and may evolve different "courtship" displays. The external characters of the females differentiate much more slowly because they are evolving at approximately the same rate as those characters of the male which are not affected by sexual selection. When such populations rejoin, they can produce hybrids because, in all essential factors, they are still genetically compatible.

The reduction or absence of sexual dimorphism in monogamous species in which the males participate in brood care is, apparently, due to two factors. In such groups sexual selection is less intense than in polygamous species and, since both adults accompany the young, the effects of predation on the male become as important as those on the female.

TAXONOMIC IMPLICATIONS

The reasons for the high incidence of monotypic genera in polygamous groups are now clear. Birds are visual animals, hence develop visible signal characters. Taxonomists utilize visible characters and emphasize differences. The degrees of difference among the males in polygamous groups are relatively large, hence the morphological taxonomist accords them generic rank.

The taxonomic significance of hybrids in polygamous groups also becomes clear. They prove the genetic compatibility of the interbreeding species, hence they prove their close relationship. Hybridization should be given far more weight as an indicator of close relationship than is given to secondary sexual characters as evidence of diversity.

If the foregoing theoretical explanation is correct, we should find highly specialized signal characters (color, pattern, voice, display) in those species which (1) are polygamous and do not form lasting pairs, and which (2) occur in sympatry with one or more related species, and which (3) occasionally form mixed pairs with one or more such related species.

Conversely, highly specific signals should be reduced or absent in species which (1) are monogamous and form a lasting pair bond and which (2) occur in isolation from species of sufficiently close relationship ever to form mixed pairs.

With these several theoretical considerations in mind we may examine some examples which appear to illustrate them.

THE BIRDS OF PARADISE (PARADISAEIDAE)

It has been suggested that the most pronounced signal characters should be found in a group of polygamous birds wherein there are several related sympatric species having short pair bonds and forming occasional hybrids. In such a group the combined effects of selection against hybrids and of sexual selection should produce a high degree of species diversity and development of signal characters in the males. These conditions are found in the birds of paradise of New Guinea.

The males of many of the 39 species of this family have long been famous for their highly specific displays, brilliant colors, plumes, and other modified feathers. Their popularity as decorative material for the millinery trade resulted in the importation of large numbers of "trade skins" to European markets. More than 100,000 were exported from New Guinea between 1870 and 1924 (Mayr, 1942:260). Among these, most of the known hybrids, some "two or three dozens," were discovered. Mayr (1945) estimates the ratio of hybrids to pure types as 1:20,000. Stresemann (1930) identified a number of hybrids which had been named as "species" and Mayr (1941) gives the parentages of known hybrids and (1942:260) discusses their significance.

In most birds of paradise the males call and display in a particular place. The females, when ready for fertilization, go to the display area, copulation occurs, and the female departs to build the nest, to incubate, and to raise the young alone. The pair bond is thus virtually non-existent since it exists only for the time required in copulation.

Ten "genera" of New Guinea birds of paradise have been involved in hydridization (Mayr, 1942:260). These apparently are the result of a female being attracted to the display ground of a male of another species. All of the hybridizing species are sexually dimorphic and all are polygamous. Three genera, *Manucodia, Phonygammus,* and *Macgregoria* have *not* been found to hybridize and are not sexually dimorphic. The solution was discovered by Rand (1938) who found that *Manucodia* forms lasting pairs and the males participate in brood care.

Evidence that sexual selection is an important factor in the evolution of male signal characters comes from at least two sources among birds of paradise. The first has been noted, namely, that the polygamous species with short pair bonds tend to be strongly sexually dimorphic, while the monogamous manucodes show a reduction of sexual dimorphism. The second piece of evidence is found in the existence of a strongly dimorphic species, Wallace's Standard Wing (*Semioptera wallacei*), living in isolation from related species in the northern Moluccas.

THE HUMMINGBIRDS (TROCHILIDAE)

The pattern of pair formation in the hummingbirds is similar to that of the birds of paradise. In most of the approximately 300 species no lasting pair bond is formed and the males are polygamous. In many species the males defend territories in which they display and to which the females come for fertilization. Species-specific displays are directed toward other males, females, and often toward other animals. The displays thus appear to be motivated primarily by hostile tendencies, that is, by escape and attack (Hinde, 1955; Moynihan, 1955), but by their specificity they can, and probably do, function as species recognition signals and hence as isolating mechanisms.

Sexual dimorphism tends to be highly developed in the species in which solitary males defend territories (Pitelka, 1942). It is certainly significant that the reduction of sexual dimorphism in the genus *Phaethornis* is accompanied by a highly vocal group display in the males. In *Phaethornis superciliosus,* for example, Nicholson (1931) and Davis (1934) have described the "singing assemblies" where several males gather to perch and call loudly in proximity to one another. Similar assemblies have been reported in *Phaethornis ruber* (Davis, 1934), *P. longuemareus* (Chapman, 1894; Skutch, 1951), and *P. guy* (Brewster and Chapman, 1895). In *Colibri thalassinus,* another species in which the sexes are alike, Wagner (1945) has described similar assemblies. In one instance 27 males were noted in an area approximately 500 meters long and 100 meters wide; sometimes two were in the same tree.

If sexual selection is operating upon these lek species of hummingbirds as, apparently, it does upon many birds of paradise, we should expect to find evidence of its effects. The sexes in *Phaethornis* and *Colibri* tend to be alike in plumage and, compared with many other genera, plumage characters are not strongly specific. There is some evidence that the pattern of the breeding biology may be of importance in this regard. In many of the species of *Phaethornis* the singing assemblies of males congregate in low, dense second-growth or thickets. In *P. longuemareus* Skutch (1951) describes a typical courtship assembly in which each male sits upon a low perch in dense cover. The tail is "wagged" while the song is repeated over and over. The assemblies of *P. superciliosus* and *P. ruber* (Nicholson, 1931; Davis, 1934) are basically similar in that the males perch for long periods and sing loudly and continually.

In these species of dense cover it appears that the vocal signals have been enhanced while in the males of genera such as *Calypte* and *Selasphorus*, which display in the open, visual signals have evolved. It is in open country species that iridescent gorgets and elaborate flight displays are most highly developed.

In most hummingbirds the females build the nest, incubate, and care for the brood alone. In two species, however, there is evidence that the males participate in brood care. Moore (1947) and Schäfer (1952) have shown that the male in *Colibri coruscans*, apparently regularly, participates in incubation and brood care; and Davis (1945) found an incubation patch in a male of *Eupetomena macroura*. In both of these species the sexes are similar in plumage.

The occurrence of hybrids in hummingbirds contains several points of interest. Of 37 hybrid combinations, recorded in the papers cited below, 25 are "intergeneric" and only five are between species of the same genus. The remaining seven are doubtful for various reasons. In these 37 hybrid combinations 28 genera are involved. Of these, 21 are sexually dimorphic, in seven the sexes are alike. Furthermore, no species of any of the so-called "hermits" (*Eutoxeres, Phaethornis, Glaucis, Threnetes, Ramphodon*) is involved (Berlioz, 1929, 1930, 1937; Butler, 1927; Hartert, 1900; Huey, 1944; Peters, 1945).

The ratio of intergeneric to intrageneric hybrids (5:1) is itself a strong indication that many of the so-called "genera" are invalid. Hummingbird genera are based largely upon the secondary sexual characters of the males (see Peters, 1945; Van Tyne, 1945). If male plumage characters have evolved originally under the impact of sexual selection, while isolated from closely related forms, it is possible that species having very different looking males are actually closely related. Their ability to hybridize should be taken as proof of close relationship, not regarded as proof that "genera" can hybridize! Hybridization may, in turn, result in further reinforcement of the male characters which function as isolating mechanisms. It is entirely possible that the ultimate result could be a pair of closely related, sympatric species with remarkably different looking males, and similar females, which occasionally produce viable hybrids.

The abnormally high incidence of monotypic genera in all classifications of hummingbirds is now understandable. Even the most recent treatment (Peters, 1945) recognizes 123 genera, of which 73 are monotypic, for 327 species. In addition, it is significant that the larger genera tend to contain groups of species in which sexual dimorphism is absent or reduced, for example, *Phaethornis* with 22 species and *Amazilia* with 29. As already suggested by Peters (*op. cit.*) the remedy for this taxonomically unsound situation is a generic classification based upon female plumages or other characters which do not function primarily as specific recognition signals. As long ago as 1909 Taylor called attention to the fact that many hummingbird genera are based upon the same characters used to differentiate species. His viewpoint was disputed by Ridgway (1909) and, unfortunately, found no protagonists. Recently Zimmer (1951:3), in a paper on Peruvian hummingbirds, has united a number of monotypic genera whose characters appear to be "of not more than specific value."

THE PHEASANTS (PHASIANIDAE)

The tribe Phasianini of the family Phasianidae is a group of 16 genera containing 49 species (Delacour, 1951). The center of distribution is southeastern Asia where up to 10 species may be sympatric. Hybrids of many combinations have been produced in captivity (Delacour, 1927, 1951) and several have been recovered in the wild (Delacour, 1948). In Europe and North America the introduced Ring-necked Pheasant (*Phasianus colchicus*) has hybridized with various native species. For example, in Europe, it has

hybridized with the Black Grouse, *Lyrurus tetrix* (Jourdain, 1912) and with the Capercaillie, *Tetrao urogallus* (Clarke, 1898; Wynne-Edwards, 1950) and in North America with the Prairie Chicken, *Tympanuchus cupido* (Lincoln, 1950) and the Ruffed Grouse, *Bonasa umbellus* (Bump *et al.*, 1947:268). Many other hybrids involving members of this family have been reported (Peterle, 1951; Hopkinson, 1926).

The degree of sexual dimorphism tends to be high, the males usually being brightly colored, the females concealingly colored in dull browns and grays. As a rule the pair bond is not a lasting one although the sexes may remain together for a longer period than that required for copulation.

Exceptions to these rules parallel the situation in *Manucodia* and *Colibri coruscans.* In the Eared Pheasant (*Crossoptilon*) the sexes are alike and the males participate in the care of the young (Delacour, 1951:188, 195), and in the Cheer Pheasant (*Catreus wallichi*), which is monogamous, sexual dimorphism is greatly reduced.

THE GROUSE (TETRAONIDAE)

The 17 species of grouse are currently contained in 10 genera, six of which are monotypic. Hybrids are frequent, all but one genus (*Centrocercus*) and at least 10 of the 17 species have hybridized with another (Peterle, 1951; Jollie, 1955). Hybrids between the Sharp-tailed Grouse (*Pedioecetes phasianellus*) and the Prairie Chicken (*Tympanuchus cupido*) are common enough to be observed with a moderate degree of frequency in the field. The hybrid between the Capercaillie (*Tetrao urogallus*) and the Black Grouse (*Lyrurus tetrix*) is of frequent occurrence in northern Europe. The male parent is usually the Black Grouse and, according to Millais (Witherby *et al.*, 1944), the hybrids result when pioneering Capercaillie females invade a new area occupied by Black Grouse before males of their own species arrive. Westerskov (1943:43) believes hybridization between these species is due to the fact that when male Capercaillie are shot out locally the females, left without mates of their own species, are attracted to the display grounds of the Black Grouse.

In most grouse the pair bond is short and the males are polygamous. In *Tympanuchus, Pedioecetes, Lyrurus,* and *Centrocercus,* the males display in a group (lek) while in *Bonasa, Lagopus,* and *Dendragapus* the males usually display singly. The Capercaillie may gather in loosely organized groups or display singly. In *Lagopus* the males are monogamous, remain near the nest, and participate in brood care and incubation.

The degree of sexual dimorphism is apparently correlated with the intensity of sexual selection. In the monogamous ptarmigan (*Lagopus*) the sexes are most alike. In the polygamous, but solitary, *Bonasa* and *Dengragapus* the sexes differ more than in *Lagopus* but less so than in the polygamous lek species of the remaining genera. In these sexual selection should be especially intense. It seems probable, therefore, that the strongly specific male secondary sexual characters in the five lek genera have evolved primarily under the influence of sexual selection. The frequent hybridization between the sympatric pairs of species is indicative of their close relationship and argues strongly for the congeneric status of *Tympanuchus* with *Pedioecetes.*

THE MANAKINS (PIPRIDAE)

The manakins include approximately 59 species usually placed in some 20 genera ranging from southern México to Argentina. In all species where life-history data are known the sexes meet only for copulation after which the female builds the nest, incubates, and cares for the young alone. The females of all species tend to be concealingly colored in shades of brown or green. Color patterns in the males are of two principal types and, in the few species for which data are available, the coloration is correlated

with the pattern of courtship and, presumably, with the intensity of sexual selection.

In the species with brightly colored males the males form courtship assemblies at certain places where they display and to which the females come for fertilization. In the Gould's Manakin, *Manacus manacus* (Chapman, 1935), the Yellow-thighed Manakin, *Pipra mentalis* (Skutch, 1949), the Blue-backed Manakin, *Chiroxiphia pareola* (Lamm, 1948), and the Lance-tailed Manakin, *C. lanceolata* (Friedmann and Smith, 1955), two or more males have been observed to display either immediately adjacent to one another (*Chiroxiphia*) or in individual "courts" spaced several feet apart.

In the Brown Manakin (*Schiffornis turdinus*), a species in which the similar sexes are dull greenish-brown in color, the males are solitary. Skutch (*in litt.*) notes that the male repeats over and over a ventriloquial, tripartite whistle as he clings to a stem in the undergrowth. Aside from this whistle there is no display. As in other manakins the male appears to take no part in the nesting or brood care.

Only one hybrid has come to my attention. This is between *M. manacus* and *Pipra erythrocephala* (Hellmayr, 1929:75). It is of interest that the males in these two species, although differing in many plumage characters, both have areas of orange-yellow on the head. It is tempting to speculate that such similar characters may have been the basis for the "mistake" in identification by the female which led to this instance of hybridization. The females of these species are extremely similar.

It is significant to the taxonomy of this group that the genera of the sexually dimorphic species have often, partly or entirely, been based upon the secondary sexual characters of the males. Examples from Hellmayr's (1910) generic diagnoses include the following genera: *Machaeropterus* Bonaparte, *Masius* Bonaparte, *Antilophia* Reichenbach, *Chiroxiphia* Cabanis, and *Chiromachaeris* Cabanis. Such characters as modified feathers, crests, color pattern, and tail length have been used as generic characters. It seems quite certain that a re-evaluation of generic limits in this family is justified.

THE GENUS ANAS

The surface-feeding ducks of the cosmopolitan genus *Anas,* as defined by Delacour and Mayr (1945, 1946), comprise 36 species which are restricted mainly to fresh water.

A pattern of pair formation somewhat different from that of preceding groups is found in this genus. Although they are monogamous, pair formation, at least in Northern Hemisphere species, occurs while the birds are in flocks during the fall, winter, and early spring. Mixed flocks of both sexes, and often of several species, congregate on the wintering ponds or lakes. Beginning as early as September, in the Mallard (*A. platyrhynchos*), the drakes perform the "courtship" displays which are associated with the formation of pairs. Sexual selection under these circumstances should be of considerable importance although possibly not as intense as in the polygamous lek groups.

In most Northern Hemisphere species there is strongly marked sexual dimorphism in plumage color and pattern but in many Southern Hemisphere species, and in all solitary forms on the smaller islands, there is little or no sexual dimorphism. The plumage patterns and colors of the females of Northern Hemisphere species tend to be composed of mottled browns, grays, black, and white which produce a cryptic pattern. The survival value of such coloration to a ground-nesting bird is obvious and has undoubtedly evolved under the selection pressure provided by predation. Only the females, as a rule, incubate and care for the young. In most species the males desert their mates when the clutch is partly complete.

In all species of *Anas* there are two molts each year. In some species the pre-nuptial molt occurs within a month or two following the post-nuptial molt. The winter plumage, which is assumed between these two molts, resembles the female plumage and is com-

monly designated the "eclipse plumage." This brings the males into nuptial plumage in the fall when pair formation begins. It seems clear that sexual selection has been an important factor in the evolution of this molt schedule.

There is fairly good evidence that the isolating mechanisms between sympatric species of *Anas* depend, at least in part, upon the female's instinctive "choice" of a male of her own species. This "choice" must depend upon innate responses because the males leave their mates before the eggs hatch, thus removing the possibility that "imprinting," or other primitive learning processes, could offer a method by which the females could learn to recognize males of their own species through early contact with their own male parent. It is likely that the combination of colors, sounds and displays (Heinroth, 1911; Lorenz, 1941, 1951) provide the basis for this innate recognition system. Males will court the females of any species. Seitz (1948) has described a similar situation in certain cichlid fishes. The males of *Tilapia heudeloti* and *T. natalensis* will direct courtship displays at the females of either species. The females, however, normally will pair only with a male of their own species. The females apparently discriminate instinctively between males on the basis of color and display movements.

Interspecific hybrids are well known in *Anas*. Their frequency and occurrence will be noted under the geographic groups of species which will follow. It will become apparent that hybrids occur with the greatest frequency between species which have a high degree of sexual dimorphism and that, on islands occupied by a single species, sexual dimorphism is reduced or absent. Where one species occurs alone the selection pressure of hybridization is absent but, presumably, sexual selection should still operate to increase sexual dimorphism. This might be interpreted to mean that the non-migratory island birds form lasting pair bonds and hence sexual selection is not sufficiently important to produce sexual dimorphism. However, at least one continental Nearctic species, the Black Duck (*A. fulvigula*), is migratory and shows a very low degree of sexual dimorphism. The correlation between lack of related sympatric species and reduction of sexual dimorphism seems to apply to the Black Duck as to the island forms. Until recently, and due to man-made habitat disturbances, the Black Duck, except for local contact with the Blue-winged Teal (*Anas discors*) was not sympatric with other species of *Anas*. The evidence thus suggests that, in *Anas*, male plumage characters function importantly as the basis of recognition by the females and are, therefore, functional as isolating mechanisms. The relative roles of sexual selection and hybridization in the evolution of plumage characters are not yet entirely clear. More information on pair bond duration in tropical and insular populations should help to clarify this problem.

THE NEARCTIC SPECIES

Nine species of *Anas* occur in North America. They are the Mallard, Pintail (*Anas acuta*), Gadwall (*A. strepera*), Green-winged Teal (*A. crecca*), Shoveller (*A. clypeata*), Blue-winged Teal, Cinnamon Teal (*A. cyanoptera*), Baldpate or American Widgeon (*A. americana*), and the Black Duck. The first eight are sympatric in the western part of the continent.

Plumage characters.—The males of each of the nine Nearctic species differ markedly from one another. The differences are especially striking among the eight widely sympatric species. Colored illustrations of these species are readily available (see Kortright, 1942; Peterson, 1947) so that detailed descriptions seem unnecessary. Since the females all look much alike, the specific characters of the males result in a high order of sexual dimorphism. From the point of view of isolating mechanisms it is important to keep in mind that it is *differences among males of sympatric species* which are significant, not merely the differences between the sexes of each species.

Hybridization.—Figure 4 indicates the extent of natural and captive hybridization among the nine Nearctic species. Captive hybrids are indicated only between species where wild hybrids are not known. Hybrid records are primarily from Phillips (1923), Delacour (1927), Rothschild and Kinnear (1929), Cockrum (1952), and Sibley (1938). Hybrid fertility is high in the crosses indicated in figure 4. The Baldpate forms sterile hybrids with all except the Gadwall. The Gadwall is thus interfertile with all of its sympatric species; the others are fertile *inter se,* except with the Baldpate.

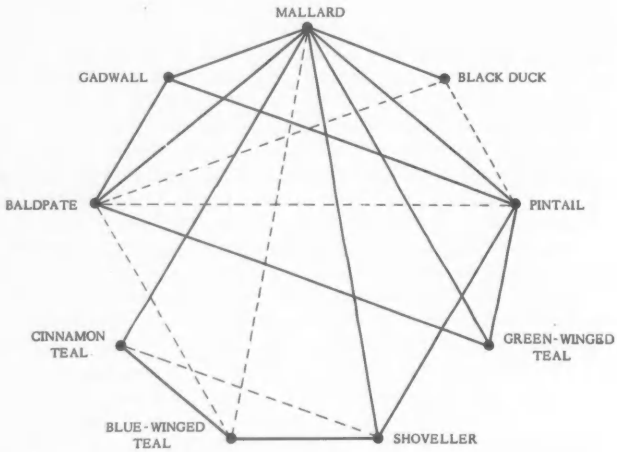

Fig. 4. Hybridization among the Nearctic species of *Anas.* Solid lines connect the parental species of wild-taken hybrids; broken lines connect the parents of hybrids bred in captivity only.

Although many specimens of hybrid ducks have been reported, their incidence is very low when the total annual hunters' kill of waterfowl is considered. Reliable data are difficult to obtain but, as one example, Hochbaum (1944:40) found one hybrid Mallard x Pintail among 1662 Mallards in checking hunters' bags at Delta, Manitoba. This is not a reliable index since hybrid females are seldom detected but it seems safe to assume that hybrid ducks, although among the more frequent natural avian hybrids, are still of uncommon occurrence. This in turn suggests that they are at a selective disadvantage in comparison with the pure parental types, even though fertility is high. Although what follows is only speculation, it may be that one reason for reduced reproductive success in the hybrids lies in the fact that their signal characters, which are utilized in pair formation, are intermediate between those of two species and hence do not "fit" either. In competition for mates the hybrids are thus placed at a disadvantage.

Nuptial display or "courtship."—Under this heading may be included all species-specific activities which, in any way, relate to pair formation. Such activities may function as intraspecific releasers in hostile encounters and also as recognition signals. For example, in most "song birds" (order Passeriformes) the males defend an area of suitable breeding habitat (= "territory") against other males of their own species. Song and

display of species-specific plumage characters and movements function both to repel other males and to attract unmated conspecific females (see Nice, 1941; Lack, 1939; Howard, 1920; Tinbergen, 1951). Tinbergen (1954) lists four functions of "courtship," namely, (1) synchronization of sexual activities in the members of a pair, (2) orientation, such as guidance of female to the song of the male, (3) suppression of non-sexual responses in the partner, such as escape and attack, and (4) reduction of interspecific mating, that is, as an isolating mechanism.

Lorenz (1941, 1951) has described the courtship movements of the males of the Mallard, Pintail, Green-winged Teal, Gadwall, and Shoveller. The displays of the Blue-winged and Cinnamon teals have been under observation by Helen Hays (personal communication). The European Widgeon (*Anas penelope*) is a close relative of the Baldpate and its display movements have been studied by Lorenz. From limited observations of Baldpate display the two appear to be very similar in their courtship movements. The Black Duck seems to be virtually identical to the Mallard in its displays.

When the courtship displays of these species are compared, it is apparent that, among sympatric species, there are differences even though the more closely related groups show strong similarities. The Mallard, Black Duck, Pintail, Gadwall, and Green-winged Teal are alike in many ways but each species (possibly excepting the Black Duck–Mallard combination) differs from the others in one or more patterns of display. The Cinnamon Teal, Blue-winged Teal, and Shoveller are similar to one another and differ widely from the Mallard type. The Baldpate is different from all of the others.

The "eclipse" plumage and time of pair-formation.—In the males of the sexually dimorphic species the plumage which follows the postnuptial molt closely resembles the plumage of the adult female. Thus it is, in general, a mottled brown pattern lacking the specific male signal characters. The flight feathers of the wing are shed simultaneously, leaving the drake flightless until they are regrown. This "eclipse" plumage is retained for periods, varying with the species, of from two to six months. A partial molt (= prenuptial) then occurs and the characteristic male plumage comes in once more. The "eclipse" plumage is thus actually the "winter plumage." What makes it special is that in some species, for example the Mallard, it is retained for only the shortest possible period of time. Thus, the drake Mallard may leave his mate in June, molt into the eclipse plumage in July, then begin the prenuptial molt in early September, regaining his nuptial plumage by October. Courtship displays begin as early as late September, even while the drakes are in the eclipse plumage. Pair bonds in the Mallard are formed by December or January (Kortright, 1942:150; Phillips, 1923:29).

There is considerable variation in the plumage and molt cycles of the males of the nine Nearctic species. The Mallard is the first to begin its courtship in the fall while the Shoveller and Blue-winged Teal do not form pairs until late winter or early spring. The other species are intermediate. Although the differences in the time of pair formation are not always pronounced, they may function as isolating mechanisms and the differences may have been enhanced through selection against hybrids. The only North American *Anas* with which the Mallard has not yet been found to hybridize in the wild is the Blue-winged Teal. The difference in the time of pair formation may be an important factor in preventing these two species from forming wild hybrids for they interbreed readily in captivity.

The "eclipse" plumage is thus simply the winter plumage which has been reduced in its duration. This has been accomplished by the shift in the occurrence of the prenuptial molt from the normal time in the spring back, in some species, to the early fall. The source of selection pressure is associated with the necessity for the drakes to be in nuptial plumage at the time of pair formation. Stresemann (1940:315) has commented

on this aspect of the plumage cycle in *Anas*. As previously noted sexual selection would tend to favor the males which regained their nuptial plumage first and would act to shift the time of the prenuptial molt. Selection against mixed pairings would tend to do the same thing since species recognition seems to depend upon the nuptial plumage characters of the males. An additional advantage is secured by the lengthening of the pair-formation period since more time is available in which to correct the mistake if mixed pairs are formed. The simultaneous shedding of the flight feathers is a mechanism which speeds up the molt cycle and returns the drakes to nuptial plumage as soon as possible. Flightlessness is not selected against since, being aquatic, the drakes are able to feed and escape from predators in the water. The desertion of his mate before the hatching of the clutch allows the drake more time to molt and, in addition, removes the non-cryptically colored drake from association with the vulnerable incubating female and flightless downy young.

ISOLATING MECHANISMS IN ANAS

It has been suggested that specific differences in (1) male plumage characters, (2) courtship display movement, and (3) the timing of the pair-formation period may function as interspecific isolating mechanisms in the sympatric Nearctic species of *Anas*. Proof of the function of plumage characters is to be sought where the hypothetical factor producing species differences is absent, namely, where only one species occurs, thus removing the selection pressure of hybridization.

In the Hawaiian Islands and on Laysan Island there occur subspecies of the Mallard. On Kerguelen Island and Crozet Island there are resident subspecies of the Pintail. The Mallards and Pintails of North America, Europe, and Asia are sexually dimorphic but in these solitary insular races the males have lost their distinctive plumage characters and both sexes have the female type of plumage. Thus, it appears that when the selection pressure afforded by the disadvantages of hybridization is removed, both sexes are able to take advantage of the selective factors producing cryptic coloration. In sympatric groups, therefore, the males are impinged upon by at least two sources of plumage-pattern-determining selection. One is predation, the other is hybridization. The first is direct, the second is via the instinctive "choice" mechanism of the female. Thus, when the female need not choose, there being no closely related sympatric species, she cannot make a mistake; the selective pressure of hybridization (interspecific responses) is removed and the male becomes cryptically colored or "feminine" under the still present and now unimpeded selection pressure from visual predators.

Mayr (1942:49, 261) has called attention to several similar situations in other insular species of birds. For example, on Rennell Island and Norfolk Island the widespread and geographically variable Whistler (*Pachycephala pectoralis*), which is usually sexually dimorphic, has evolved "feminine" races. As Mayr notes, such situations occur only where no similar species exist. The identity of the interacting species in this instance has not been determined. There is no way to predict how it will look or sound, except that it must be different from the species which it affects by its presence. Its identity may be revealed by a study of the species which are present or absent on various islands in relation to the distribution of the "feminine" races. Lack (1945:62–63) cites other examples.

Vaurie (1951) has described an interesting situation which illustrates this same principle. *Sitta neumayer* and *Sitta tephronota* are rock nuthatches occurring in southwestern Asia. Each species has a large distribution and over most of the ranges they are allopatric. At the extremes of their respective ranges, where each is far removed from the other, the two are remarkably similar in facial markings and bill size. In one region

the two species are sympatric. In this area of sympatry each has diverged, in opposite ways, from the similar pattern they possess when allopatric. One has developed a black facial "mask," in the other the facial area has become paler. The bill size is similar in the allopatric forms but in the area of overlap one has evolved a larger bill and the other a smaller bill. The facial markings apparently function in species recognition; the difference in bill size is advantageous in reducing competition for food.

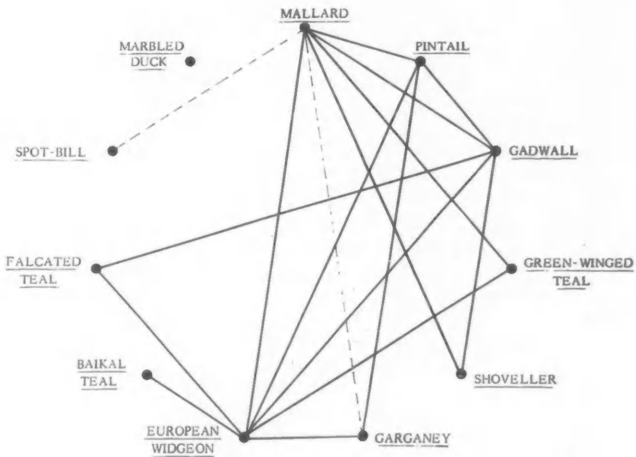

Fig. 5. Hybridization among the Palearctic species of *Anas*. Solid lines connect the parental species of wild-taken hybrids; broken lines connect the parents of hybrids bred in captivity only.

There is no direct evidence to prove that "courtship" movements function as isolating mechanisms. The fact that they vary specifically in sympatric groups of species suggests that they do so. However, the fact that they are most similar in the most closely related species such as Mallard, Pintail, Gadwall, Cinnamon Teal, Blue-winged Teal, and Shoveller suggests that the movements *per se* may function importantly in hostile responses between males and that the patterns of color and structure revealed or brought into prominence by the movements are more important as isolating mechanisms. The timing of pair formation, in its role as an isolating mechanism, has been discussed previously.

Palearctic species.—In the Palearctic there occur 11 species of *Anas*. Figure 5 indicates the known occurrence of hybrids. As in the Nearctic species the male plumages and nuptial displays are species-specific and the timing of pair formation is variable. The Mallard is the earliest in forming pairs and the Garganey (*A. querquedula*), a close relative of the Blue-winged Teal, is the latest. It appears that the Palearctic group of sympatric species is similar with respect to isolating mechanisms to the Nearctic group.

Southern-hemisphere species.—In the course of this study the South American, African, and Australasian species of *Anas* were investigated. Information on many aspects

of the problem is lacking and, from some areas, reports are conflicting. It is, therefore, difficult to assess the significance of variational patterns but several items are of interest.

In many species in South America and Africa there is a tendency for sexual dimorphism to be slight or lacking. If our premises are correct this condition may indicate that both interspecific reactions (hybridization) and intraspecific reactions (sexual selection) are reduced in intensity. Such reduction in these sources of selection could be achieved by an increase in the degree of ecological isolation among seemingly sympatric species and in the establishment of a permanent pair bond. Skutch (1940:502) has suggested that the existence of permanent pair bonds in tropical species may account for the reduction in sexual dimorphism in some instances. There seems to be no proof that this is a factor affecting tropical species of *Anas* but, at least in non-migratory species, pairs may remain together more than in the strongly migratory Holarctic species. Information on this problem is needed.

South American species.—The nine species of *Anas* in South America are the Bronze-winged Duck (*A. specularis*), Versicolor Teal (*A. versicolor*), Bahama Duck (*A. bahamensis*), South American Pintail (*A. georgica*), Yellow-billed Teal (*A. flavirostris*), Chiloe Widgeon (*A. sibilatrix*), Cinnamon Teal (*A. cyanoptera*), South American Shoveller (*A. platalea*), and the Ringed Teal (*A. leucophrys*). Two species (*specularis* and *leucophrys*) are somewhat aberrant; the other seven are typical *Anas.*

Each of the nine species overlaps with one or more of the others in some portion of its range. As many as eight species occur sympatrically in certain parts of the continent.

The information on wild hybrids is extremely meagre. The only record is of a Bahama Duck x South American Pintail (Phillips, 1923:338) taken near Buenos Aires in 1914. Hybrids between the similar species might well go undetected and the paucity of informed hunters, "bag checks" by game wardens, and other factors which act to bring hybrids to the attention of scientists in North America make it likely that this is not a ratio comparable to that for North America.

In captivity the following hybrids have been recorded. Versicolor Teal x Baikal Teal; Bahama Duck x Mallard; Bahama Duck x Brazilian Teal (*Amazonetta brasiliensis*); Bahama Duck x South American Pintail; South American Pintail x Wood Duck (*Aix sponsa*); Yellow-billed Teal x Mallard; Yellow-billed Teal x Chestnut-breasted Teal (*Anas castanea*); Chiloe Widgeon x Mallard; Chiloe Widgeon x European Widgeon; Chiloe Widgeon x Wood Duck; Ringed Teal x Brazilian Teal.

These hybrids indicate that at least these six species are capable of forming mixed pairs under certain conditions. The Cinnamon Teal of South America may be assumed to be similar to the North American populations in this respect, making seven of the nine South American *Anas* which have been known to form hybrids with some other species.

The Cinnamon Teal, South American Shoveller, and Ringed Teal are strongly sexually dimorphic. In the Chiloe Widgeon and Bronze-winged Duck both sexes are brightly colored. The other four species exhibit a tendency toward reduction of sexual dimorphism, the males being less, the females more, brightly colored than in most Northern Hemisphere species. The Bahama Duck and the Versicolor Teal are similar in color pattern but differ greatly in body size and bill color. The South American Pintail resembles the Yellow-billed Teal in coloration but Lorenz has found that the courtship movements are extremely different in the two. The display of the Versicolor Teal has not been studied but that of the Bahama Duck includes the most highly specific "head-up-tail-up" movement of any of the species of *Anas* which have been investigated.

Solitary insular forms again provide evidence of the loss of signal characters in isolated species. In the Galapagos Islands subspecies of the Bahama Duck (*A. b. galapag-*

ensis) and the South Georgia Island race of the South American Pintail (*A. g. georgica*), the species-specific markings are reduced as compared with the mainland populations. The Galapagos Bahama Duck has the white facial area reduced in size and brightness and the South Georgia Pintail has a gray bill in marked contrast to the bright yellow bill of the continental races. They thus exhibit the same tendency toward a "feminine" coloration as in the Hawaiian Mallard, Kerguelen Pintail, and others. This is interpreted as evidence that these characters function as "recognition signals" and hence are isolating mechanisms in areas of sympatry with close relatives.

African species.—In Africa the genus *Anas* is found primarily in the southern and eastern portions of the continent. The species are the Cape Teal (*A. capensis*), Hottentot Teal (*A. punctata*), Red-billed Duck (*A. erythrorhyncha*), Madagascan Teal (*A. bernieri*), Meller Duck (*A. melleri*), Yellow-billed Duck (*A. undulata*), African Black Duck (*A. sparsa*), and the Cape Shoveller (*A. smithi*). Two species (*bernieri* and *melleri*) are confined to Madagascar and two others (*punctata* and *erythrorhyncha*) occur both on the mainland and on Madagascar. The other four species occur only on the mainland. Thus there are four species on Madagascar and six on the mainland.

The tendency for sexual dimorphism to be reduced is extremely pronounced. The Cape Shoveller is the only African species which is dimorphic and it is but weakly so. The other species show no important degree of difference between the sexes in plumage color or pattern and all tend toward a cryptic plumage pattern.

In Africa not more than six species may be sympatric. Of these the African Black Duck is a solitary stream-dwelling species which is thus ecologically well separated from its congeners. The other five species are separable from one another by plumage patterns but to a lesser degree than in the males of Holarctic species. There is, however, apparently a tendency for these species to segregate ecologically to a greater degree than do the Holarctic sexually dimorphic species. Phillips indicates that the Cape Teal is partial to the larger lakes, the Hottentot Teal is most common in the mountains, the Red-billed Duck inhabits swamps and rushy pools, and the Yellow-billed Duck is most abundant on lakes and rivers in open country.

Thus, in comparison with the Holarctic species, there are in Africa fewer sympatric species and these are to some degree isolated ecologically from one another. These factors act to reduce the opportunity for the formation of mixed pairs. This in turn has apparently reduced the pressure of selection from this factor and permitted the various species to respond to the forces of selection producing concealing patterns of color. The result is a group of species with a tendency toward a plumage type in both sexes such as is found in the females of Northern Hemisphere species and which reaches its extreme development in insular species where no congeners are present. Information on the duration of pair bonds is not available.

No wild-taken hybrids have been recorded. In captivity the Meller Duck x Mallard produced fertile offspring (Phillips, 1923:128). The Yellow-billed Duck has been crossed with Mallard, Red-billed Duck, North American Black Duck, and Spot-billed Duck (*A. poecilorhyncha*). A female African Black Duck in the London Zoo formed a pair with a Spot-bill but reared no young (Delacour, *in litt.*).

Lorenz has studied the Meller Duck and the Red-billed Duck. The Meller Duck is extremely similar to Mallards but more pugnacious. It is of interest that in this sexually monomorphic species, females are especially prone to mate with drakes of other species in captivity, even when their own drakes are present. This, as Lorenz (1951) points out, is certainly connected with the lack of a distinctive male plumage. The females of this insular species, which presumably evolved as an isolated population of ancestral Mallard stock, apparently have their pair-formation responses adjusted pri-

marily for patterns of movement. It may be that the strong colors and patterns of Holarctic drakes function as "supernormal releasers" (Tinbergen, 1951), that is, they stimulate the innate responses of the females more strongly than the "normal" releasers contained in the plumage patterns of drakes of their own species.

There are additional situations in *Anas* which merit attention but these few will serve to illustrate some of the aspects of the problem. Information about Australasian species is difficult to assess. Perhaps resident ornithologists in that region will know of situations which parallel those noted herein.

DISCUSSION

The examples which have been cited were chosen to illustrate groups in which sexual dimorphism is present, hybrids are occasional, polygamy is usually present, and genera are often based on male signal characters. These various conditions do not invariably accompany one another and, to be complete, such groups as the sunbirds (Nectariniidae), wood warblers (Parulidae), and tanagers (Thraupinae) should be considered. In these sexual dimorphism is often pronounced but monogamy is the rule and the males tend to participate in brood care, although not in incubation. It is obvious that other sources of selection, possibly associated with inter-male competition for territories, are important.

I have tried to show why, at the generic level, taxonomists have tended to oversplit groups with a high degree of sexual dimorphism in visible characters. The opposite effect is demonstrable in groups having little or no sexual dimorphism in such characters. In birds which are nocturnal, or which live in dense cover, visual signals are of less value while sounds become more so. In such groups there is a tendency to evolve highly specific songs or calls but to reduce the specific diversity in plumage characters. This is reflected at the generic level by a decrease in the number of monotypic genera and an increase in the number of species per genus in such groups. The following are examples.

The owls (Strigidae), which seem to utilize sound more than sight in species and sexual recognition, have 27 genera for 123 species (4.5 species per genus). The goatsuckers (Caprimulgidae) have 19 genera and 67 species (3.5 species per genus). The genus *Caprimulgus* alone contains 39 species. The ant-thrushes (Formicariidae) are mostly thicket-dwelling birds; the family contains 221 species in 53 genera (4.2 species per genus). The wrens (Troglodytidae) with 16 genera and 63 species (4.0 species per genus) are also a group which apparently utilizes sound more than sight in species recognition.

In comparison consider the number of species per genus in the following groups: Hummingbirds (Trochilidae), 2.6 species per genus; grouse (Tetraonidae), 1.6 species per genus; manakins (Pipridae), 3.0 species per genus; and birds of paradise (Paradiseidae), 2.4 species per genus. These data are derived from Peters (1945), Hellmayr (1929), and Mayr and Amadon (1951).

In the Anatidae, Peters (1931) recognized 62 genera for 167 species (2.7 species per genus). In their revision of the Anatidae, Delacour and Mayr (1945) reduced the genera to 40 and the species to 144 (3.6 species per genus). In the process a considerable number of "intergeneric" hybrids became intrageneric.

SUMMARY

The process of speciation is accomplished through the accumulation of genetic differences in spatially isolated populations. If intrinsic isolating mechanisms evolve before the extrinsic barriers break down, the secondarily rejoined populations can exist in sympatry as good species. If the extrinsic barrier fails before intrinsic barriers are fully established the resulting hybridization will have different effects, depending upon the relative biological success of the hybrids. If the hybrids are not at a selective disadvan-

tage compared with the parental populations, the result will be introgression leading to ultimate swamping and, following a period of increased variability, a new adaptive peak will become established.

If the hybrids are selected against, they function as a selective force against the individuals of both parental populations which enter into hybrid pairs. Any mechanism which reduces the incidence of mixed pairs is thus selected for with the result that, as long as the hybridization continues, the isolating mechanisms of the parental species are reinforced relative to one another. Reinforcement ceases when interspecific reactions relative to pair formation cease. This may be some time after hybrids are no longer produced.

The reinforcement of isolating mechanisms in animals which utilize visual signal characters in pair formation results in the enhancement of visible structures and associated behavior patterns. Birds are especially fine subjects for study in this connection. In most birds the females instinctively "choose" males of their own species as mates. The choice mechanism depends upon the stimulation of the innate releasing mechanisms of the females by the species-specific signal characters ("releasers") of males of their own species. It is these signal characters, or isolating mechanisms, which are enhanced by the reinforcement which occurs when interspecific hybrids are selected against.

In groups of closely related species where hybridization occurs, but is selected against, the males develop "exaggerated" signal characters. In certain instances the males of insular populations, which occur in isolation from any closely related interacting species, have lost their signal characters and become "feminine." This is due to the fact that the females cannot make a mistake in mate choice, there being only one species present, and thus the selective effects of hybridization are removed.

A second source of selection which increases the development of signal characters is derived from the competition for mates. This "sexual selection" is an intraspecific phenomenon and is especially important in polygamous species. Since only the secondary sexual characters of the males (in most groups) are affected, the result is an increase in sexual dimorphism. The males of related species tend to diverge rapidly while the females remain similar. Secondary contacts between such pairs of species may result in hybridization because the degree of relationship is actually very close.

The high incidence of monotypic genera in groups of sexually dimorphic visual animals is due to erroneous human evaluation of the taxonomic value of signal characters. Morphological structures evolved under the selection pressure of deleterious hybridization and/or sexual selection seem highly "specialized" to the intelligent discrimination of the human taxonomist who therefore accords them generic rank on a "degree of difference" basis. This is a coincidental result of the fact that we too are visual animals and hence can and do utilize visible characters in taxonomy. It is significant that "intergeneric" hybrids are found almost exclusively in visual animals, principally birds and, to some extent, fish. It is apparent that genera in such groups should not be based only upon secondary sexual characters nor upon characters which have been reinforced by selection against hybrids since these, inevitably, are *species* characters.

ACKNOWLEDGMENTS

Studies contributing to this paper have been, or are being, supported by the American Philosophical Society, the National Science Foundation, and the Graduate School and College of Agriculture of Cornell University.

For comments and suggestions I am indebted to Ernst Mayr, Konrad Lorenz, Jean Delacour, Martin Moynihan, S. Dillon Ripley, Peter Marler, Peter Scott, E. Thomas Gilliard, William C. Dilger, and many others.

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THE INFLUENCE OF A HAWK'S APPETITE ON MOBBING

By FRANCES HAMERSTROM

Falconers who watch closely the appetites of their hawks to determine whether or not birds are "sharp set" (hungry) enough to fly at game are often amused by paintings of hawks with feathers and attitude of the body showing repose bordering upon somnolence but with talons "fiercely" clutching prey. If a competent falconer can detect at a glance a raptor's mood—to hunt or not to hunt—it seems probable that prey species can do the same as well or better.

To test the influence of a hawk's appetite on the mobbing reaction of small birds, I conducted a series of experiments with a tame male Red-tailed Hawk (*Buteo jamaicensis*), which was taken on May 27, 1956, when almost ready to leave the nest and which was trained to fly to the fist. Twenty-six testing stations were set up near Plainfield, Wisconsin. Two five-minute tests were run at each station: one with the hawk well fed and the other with him "sharp set." For each test the hawk was tethered to a perch three to five feet in height and reactions of prey species were watched from a convenient distance. Station 1 was in the woods and the remainder of the stations were in open country but near brush, woods or marshes. After every five to eight tests the hawk was rested, thus four groups of tests were run in pairs (fed and "sharp set") until all 26 stations had been covered.

The behavior of the hawk during tests seemed rather similar whether "sharp set" or well fed. He remained in motion most of the time, either moving his head, shifting position, plucking at his feet or jesses, or occasionally sunning with outspread wings, but he did not often attempt to leave the perch. His few attempts to leave seemed to be for the purpose of seeking another perch rather than for taking off after prey.

When well fed, the hawk was mobbed at eight of the 26 stations; when "sharp set," he was mobbed at 14 of these same stations. See table 1.

Table 1

Summary of Mobbing

Date	Stations								
					Well Fed				
Aug. 2	1–7	mob	....	....	mob	....	....	....	
Aug. 4	8–13	....	....	mob	mob	mob	....		
Aug. 9	14–18	....	....	....	....	....			
Aug. 13	19–26	mob	....	mob	....	....	....	mob	....
					Sharp Set				
Aug. 3	1–7	mob	mob	....	mob	crowd	mob	....	
Aug. 5	8–13*	....	....	mob	mob	....	....		
Aug. 9	14–18	....	mob	....	crowd	....			
Aug. 11	19–26	mob	....	....	mob	....	crowd	crowd	crowd

* On August 5, I apparently misjudged the condition of my hawk. Immediately after the last test he refused to fly to the fist, took off, and disappeared until August 9 when I caught him again. This behavior indicates that he was not very "sharp set" which may account for the paucity of reactions on this day.

Mobbing was of two types: (1) one or two birds of the same species got excited or (2) a mixed crowd showed agitation. Altmann (Condor, 58, 1956:241–253) made a similar observation. When fed, the hawk never drew a crowd, but when "sharp set," he was mobbed by aggregations at five stations. Aggregations were hard to count but consisted of about 10 to 40 individuals. Details are summarized as follows:

Hawk well fed.—Species which initiated mobbing: Ruby-throated Hummingbird (*Archilochus colubris*) buzzed around head; Black-capped Chickadee (*Parus atricapillus*), called "chickadee"; Scarlet Tanager (*Piranga erythromelas*) sang; warblers (Parulidae) scolded; Catbird (*Dumetella carolinensis*) gave mews; English Sparrow (*Passer domesticus*) chirped and circled; Eastern Kingbird (*Tyrannus tyrannus*) dove and hit head.

Hawk sharp set.—Species which initiated mobbing: Robin (*Turdus migratorius*) scolded; Indigo Bunting (*Passerina cyanea*) gave chips; Downy Woodpecker (*Dendrocopos pubescens*) repeated alarm notes; American Goldfinches (*Spinus tristis*) uttered jay-like cries from nearby bush; Ruby-throated Hummingbird, Catbird, Scarlet Tanager, warblers, and English Sparrows.

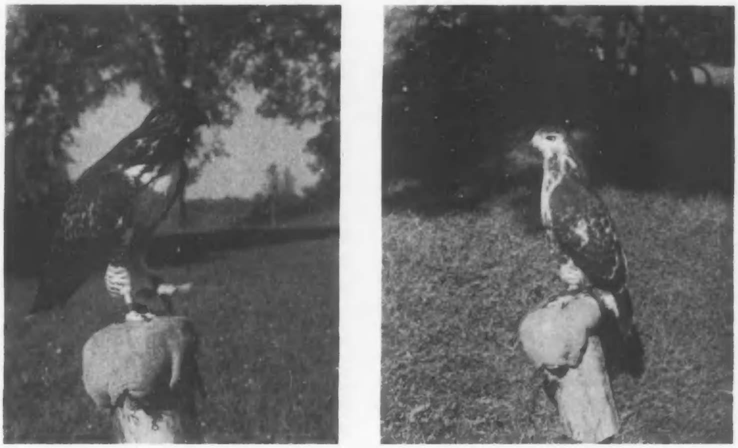


Fig. 1. Tame Red-tailed Hawk, showing different attitudes related to hunger. Left, well fed; right, hungry or "sharp set."

Stations where the Black-capped Chickadee, Scarlet Tanager, and Catbird reacted were revisited, following the usual procedure, but without the hawk, because at these particular stations I was in doubt as to whether or not I had induced the mobbing. In no case did the prey species react to me alone.

Species which mobbed after another species had started mobbing (this occurred only when the hawk was "sharp set") were: Song Sparrow (*Melospiza melodia*), House Wren (*Troglodytes aëdon*), vireos (Vireonidae), Eastern Kingbird, warblers, English Sparrow, Indigo Bunting, and Red-headed Woodpecker (*Melanerpes erythrocephalus*).

It is quite plain that the presence of a hawk does not guarantee a mobbing reaction. At ten stations the hawk was not mobbed in the course of the two test runs. Birds observed at this time in the near vicinity were as follows: Blue Jay (*Cyanocitta cristata*), Song Sparrow, Catbird, and Cedar Waxwing (*Bombycilla cedrorum*), at one station each; Eastern Kingbirds at three stations and American Goldfinches at five with the hawk well fed; Eastern Kingbird, Mourning Dove (*Zenaidura macroura*), and Song Sparrow at one station each, and American Goldfinches at five stations with the hawk "sharp set."

Beginning in early July, I flew the hawk outdoors nearly every other day. He was trained to come to my fist for food when I whistled, although the sight of the glove was sometimes enough to bring him in. At first I only attempted short flights of about 20 yards from one person to another, but progressively I permitted him more freedom and not infrequently left him at liberty for hours at a time. These flights were not counted

as they were not part of the experiment proper but were merely to keep the bird in top notch condition. They did, however, give me an opportunity to observe mobbing under more natural circumstances.

It seemed clear that the hawk elicited far less mobbing when he was tethered to relatively low perches in the course of the tests than when he was on the high perches he selected when "sharp set." Whenever he disappeared while I was flying him "sharp set," I could find him again within a few minutes by listening for the mobbing and scanning conspicuous perches nearby. When he escaped well fed, I heard no mobbing and he was not to be found on his usual high perches. Under these circumstances I was able to find him only once before he returned of his own accord with an appetite sufficient to bring him to my fist. Upon this occasion he was sitting near the center of a large tree and there was no mobbing. While flying at about treetop height or lower, he was invariably mobbed whether "sharp set" or fed. When he was soaring high, I saw no mobsters.

The appearance of a hawk that is well fed in contrast to "sharp set" needs further analysis. Tentatively, I suggest that when in the well fed condition the head and eyes appear rounder. A healthy hawk standing on one foot with the other foot tucked up under his feathers is not inclined to hunt. In a "sharp set" Red-tail, the top of the head often appears flattened with the hind neck feathers erected, the wings tend to be held higher, the superciliary stripes seem straighter and seem to form overhanging ledges; slight head motions forward often indicate a readiness to hunt. It might be stated at this point that young Cooper Hawks (*Accipiter cooperii*), when they are not quite fully feathered, appear to show considerably more expanse of white down when hungry. This may have survival value in that it could lead the parents to feed the hungriest and most conspicuous youngster first. It may be that a study of feather positions in young, incompletely feathered hawks, fed and unfed, might facilitate recognition of the presumably more subtle differences in older hawks.

Conditioned mobbing was a curious by-product of this study. The robins present in the locality where I always flew my hawk, having heard me whistle him in to my fist repeatedly early in the summer, apparently came to associate my whistle with the arrival of a hawk. I noticed this first on August 6 when my hawk had disappeared for a time. Thereafter the robins mobbed consistently whenever I whistled, even though no hawk was coming. Robins tested with the same whistle at five other localities gave no response.

In the course of the tests the fed hawk was mobbed by 12 individuals. "Sharp set," he was mobbed by about 100. The crowds attracted when he was "sharp set" are probably attributable to more persistent initial mobbing which attracted other birds to mob rather than to his "sharp set" appearance *per se*. The conditioned robins, responding to my whistle with no hawk present, sometimes drew a crowd.

SUMMARY

A male Red-tailed Hawk attracted more mobbing when "sharp set" (hungry) than when well fed. When fed, it was mobbed at eight of 26 test stations and attracted no aggregations. When "sharp set," it was mobbed at 14 of the same stations and attracted aggregations at five of these. At ten of the 26 stations it was not mobbed.

The hawk was mobbed more consistently at the high perches he selected for himself when "sharp set" than at the perches three to five feet high to which he was tethered at test stations.

He was mobbed most consistently when flying low, but he was never mobbed when soaring.

Conditioned mobbing was observed.

State of Wisconsin Conservation Department, Plainfield, Wisconsin, November 10, 1956.

DETERMINATION OF AGE IN THE SPOTTED TOWHEE

By JOHN DAVIS

The segregation of series of birds into age classes is of paramount importance to the avian taxonomist, physiologist, and student of bird behavior and ecology. In passerines, age groups have been shown to differ in measurements (for example, *Aphelocoma*, Pitelka, 1951:199; *Pipilo erythrophthalmus*, Sibley, 1950:115) and in physiology (*Agelaius phoeniceus*, Wright and Wright, 1944:49–55). Pitelka (1945:256) stated that age classes in *Aphelocoma* differ so widely in the measurements of structures used in taxonomy that "any work on the systematics of corvids in which first-year specimens are not distinguished from adults is at once suspect." The importance of age determination of individuals to the scientist investigating the behavior and ecology of banded birds is so obvious as to require no further comment here.

In the present study 123 males and 70 females of the Spotted Towhee (*Pipilo erythrophthalmus*) were collected over a 16-month period in order to determine the annual reproductive cycles. All birds were taken within three miles of the Hastings Reservation, northern Monterey County, California, and were members of a continuous population of the subspecies *P. e. megalonyx*. Since the skin of each bird was saved, there is available a large series representing first-year and adult birds taken in every month of the year, from which information can be derived as to the morphological differences between age groups. Most of the criteria for determining age were derived from series of 14 adult and 14 first-year males and nine adult and four first-year females, all collected in the fall and early winter when first-year individuals could be distinguished by the incompleteness of the apparent double-walling of the skull. Other criteria were established by using the entire series of males and females.

Criteria now in use.—Dwight (1900:207), working with northeastern populations of *Pipilo erythrophthalmus*, stated that the postjuvenal molt of this species is partial, first-year birds retaining the primaries, the primary coverts, and the secondaries. "Young and old become almost indistinguishable except by the browner primary coverts of the young birds."

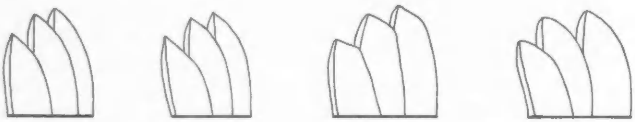
Sibley (1950:114), working with western and Mexican races of *P. erythrophthalmus*, used the contrast between the retained, brownish primary coverts and the fresh, black secondary coverts to distinguish first-year males. In adult males both the primary and the secondary coverts are black. He stated that the contrast between the two series of coverts in females was "not great enough to permit dependable age determination."

In the series at hand, the criterion of the color of the primary coverts is of great value in differentiating first-year males. Females can actually be differentiated on this character, the coverts of adults ranging from dark gray to black. However, by midwinter the primary coverts of most females have oxidized to a brownish hue that is similar to that of the coverts of first-year birds. The usefulness of this character in females thus lies chiefly within the period during which age can be determined by the degree of skull ossification, but it may be applied to fall and winter specimens for which information on skull characters is lacking.

Swarth (1905:172) stated that the rumps of first-year male *P. e. megalonyx* are grayish, whereas the rumps of adults are black. In the series at hand, the average rump color of first-year birds is paler and grayer than that of adults. However, there is considerable variation in this character within each age class, and the overlap between them is too great to permit the use of rump color as a criterion for determining age.

The specimens at hand indicate that there are other useful characters for establishing age in the Spotted Towhee. These are of particular value in connection with the ages

of females, but they serve also to corroborate the ages of males which have been classified on the basis of the color of the primary coverts. As Emlen (1936:102) has stated for *Corvus brachyrhynchos,* and Pitelka (1945:256) for *Aphelocoma,* the characters distinguishing first-year birds from adults should not be used individually, but in combination. The following characters can be combined with primary covert color to determine age.



a. b. c. d.

Fig. 1. Shape of lateral rectrices of *Pipilo erythrophthalmus megalonyx* collected near the Hastings Reservation, Monterey County, California. *a,* juvenal female, July 6, 1955; *b,* first-year male, September 28, 1955; *c,* adult male, November 26, 1955; *d,* adult male, December 22, 1955.

Shape of the rectrices.—The material at hand presents concrete evidence that in the great majority of first-year birds the rectrices are not lost at the postjuvenal molt. When the series of 14 known adult and 14 known first-year males are compared, two differences in the rectrices are obvious. First, the rectrices of the adults are considerably less worn. Second, the tips of the rectrices of the first-year birds are rounded or pointed, whereas those of the adults are noticeably blunt or truncate (fig. 1). The difference in shape is especially evident in the three outer rectrices, and most consistently in rectrices 4 and 5. Two first-year males are of particular interest. Number 70, collected on December 5, 1955, had evidently suffered a previous accident to its tail, as rectrices 1–6 on the right side and rectrix 1 on the left side are being replaced. The rectrices of the left side are pointed whereas those of the right side are truncate. Number 90, collected on January 26, 1956, with the skull about nine-tenths ossified, has replaced rectrices 4–6 on the right side, these feathers being much less worn than their counterparts on the left side. Rectrices 5 and 6 of the right side are pointed, but rectrix 4 is truncate. This would indicate that all replaced juvenal rectrices are not necessarily of adult configuration.

To test the value of these characters, the two series of males were intermingled and the flat skins placed in a pile. It took exactly 90 seconds to sort out the 14 immatures, without error, on the basis of shape and wear of the rectrices. The same differences in wear and configuration are evident in the rectrices of first-year and adult females.

However, the rectrices of adults are not invariably truncate (fig. 1d). The situation is similar to that described for *Aphelocoma* by Pitelka (1945:256), in which the "adult rectrices are not necessarily truncate and, indeed, may be strongly suggestive of juvenal feathers," although such similarity was found to be "comparatively rare," as it is in the series of *megalonyx.* In using this character, some confusion may arise because of rectrices adventitiously replaced by first-year birds, but such replacement is usually obvious because of its asymmetry.

The shape of the tail itself does not serve to separate age classes in the Spotted Towhee. Emlen (1936:101) found that the tails of first-year American Crows were rather square whereas those of adults were rounded. This was reflected in measurements of the difference in length between the central rectrices and the next to outermost rectrices. Pitelka (1945:255), using the same measurement, demonstrated this differ-

ence between age classes in *Aphelocoma*. In the Spotted Towhee the shape of the tail varies so widely within each age class that it is not useful in determining the age of an individual.

Table 1

Width of White Spot on Rectrix 4

Age Determined on Skull Characters Only

Age	Sex	N	Range	Mean	Standard error	Standard deviation
First-year	♂	13	0.0– 7.1	3.13	±0.55	1.98
Adult	♂	12	5.1–10.4	7.62	±0.46	1.58
First-year	♀	4	0.0– 2.6	1.05	....	....
Adult	♀	9	1.9– 9.9	6.29	....	....

Age Determined on Skull and Plumage Characters in All Months

Age	Sex	N	Range	Mean	Standard error	Standard deviation
First-year	♂	39	0.0–10.4	3.20	±0.42	2.60
Adult	♂	52	0.0–10.4	7.11	±0.25	1.84
First-year	♀	24	0.0– 5.4	1.71	±0.32	1.58
Adult	♀	37	0.0–10.1	5.89	±0.44	2.71

The retention of the rectrices by first-year *P. e. megalonyx* differs from the situation described for the nominate race in New York (Dwight, 1900:207) and Michigan (Sutton, 1935:17–18) and indicates that there is geographic variation in the extent of the postjuvenal molt. In this species, as thus far investigated, the resident birds retain the rectrices, and the migratory form replaces them.

The failure of first-year *megalonyx* to molt the rectrices is also of interest as regards the intrageneric relationships in *Pipilo*. It has been suggested that the Brown Towhee (*Pipilo fuscus*) and its allies are possibly not congeneric with *P. erythrophthalmus* and its allies (Coues, 1866:89; Davis, 1951:10, 100–101). Most immature *P. fuscus* retain the rectrices through the first year, and their rectrices are noticeably more rounded and less truncate than those of adults (Davis, *op. cit.*:3). The interspecific variation in the extent of the postjuvenal molt is apparently bridged by at least some of the western populations of *Pipilo erythrophthalmus*.

Tail spotting.—First-year and adult birds of both sexes differ in the width of the white spot on rectrix 4. The spot is, on the average, much narrower in first-year birds, and in many it is either absent or reduced to a narrow streak. In making measurements, when the spots were of different widths on the left and right fourth rectrices, the wider spot was always measured, except that if a fourth rectrix had been replaced adventitiously by any first-year bird, the spot on the replaced feather was not measured.

Measurements were made initially on the adults and first-year birds the ages of which had been determined on skull characters; subsequently it was made on all birds aged by plumage and/or skull characters. The two sets of data are presented in table 1, and those pertaining to the larger series are shown graphically in figure 2. In the smaller series the means for the males of the two age groups are separated by two standard deviations. In the larger series the means for both sexes are separated by five standard errors, and the average differences between adults and first-year birds are statistically significant. Reference to figure 2 will show that the white spot was absent on rectrix 4 in only one adult male of 52 (1.9 per cent) whereas it was absent in eight first-year males of 39 (20.5 per cent). For the females, the corresponding figures are one of 37

adults (2.7 per cent) and eight of 24 immatures (33.3 per cent). In the males a rather sharp break occurs at 6 mm. Eight of 52 adults (15.4 per cent) fall below this figure, and six of 39 immatures (15.4 per cent) lie above it. In the females, the break occurs at 3 mm.; four of 37 adults (10.8 per cent) fall below this figure, and three of 24 first-year females (12.5 per cent) lie above it. It seems apparent that, while not completely reliable, this plumage character can be of considerable value in determining age.

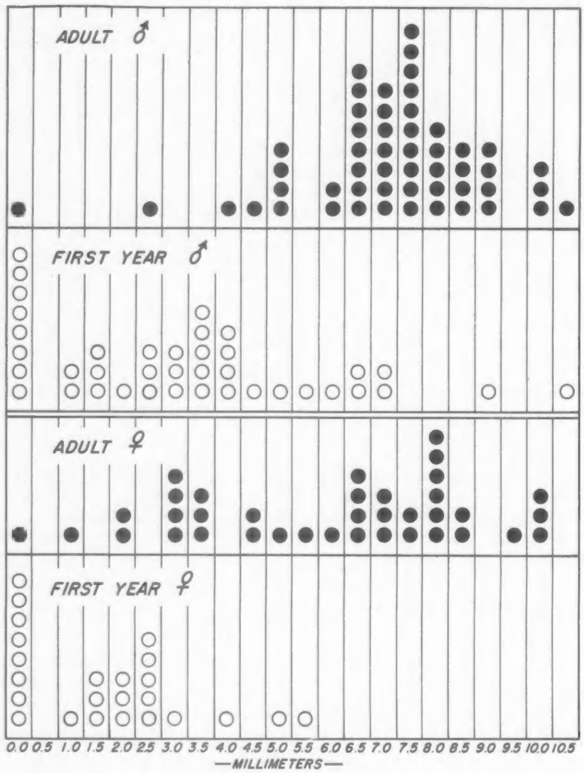


Fig. 2. Frequency of measurements of width of white spot on rectrix 4 in birds taken in all months.

Seven first-year birds have replaced rectrix 4 on one side. The measurements in millimeters of the width of the white spot on the replaced rectrix and the retained rectrix are as follows (replaced rectrix first): 6.4, 2.1; 8.7, 1.9; 7.8, 2.4; 4.8, 0.0; 5.6, 2.5; 4.0, 0.0; 0.0, 0.0. In only one of the seven birds has the replaced rectrix 4 failed to bear a larger white spot; this was in an individual lacking spots on both the new and the old feathers.

It is difficult to ascertain the adaptive significance of increased white spotting on

rectrix 4 in adults. The spot averages larger in males than in females, but the average difference is not statistically significant. Further, the increase of the white spotting in adults occurs in both sexes. These facts suggest that the spots are not used in any courtship display, and I have never seen any such display in this species. If the assumption is made that more adults than first-year birds are paired during the breeding season, as seems likely, then it may be that the white tail spots are used in threat displays in defense of territory, or as an indicator of location or position between the members of a pair. I have never seen the tail used in any threat display in a number of territorial clashes involving both sexes. However, Spotted Towhees frequently flirt the tail when hopping, and females returning to the nest often perch near it for a few seconds, flipping and flirting the tail, before going down to the eggs or young. Spotted Towhees frequently spread the tail when they take flight. Grinnell and Storer (1924:478) noted that "even then their broken pattern of coloration would be protective in effect were it not for their almost incessant activity. But when a towhee takes flight from one thicket to another its brilliant coloration flashes forth vividly; a predominance of black is seen, but the white dots on the shoulders and wings, and the white 'thumb marks' at the end of the fan-shaped spread tail, introduce a decided element of contrast." The use of the tail in these ways suggests that brief, intermittent display of the tail spots serves as an indicator of position, and this would be of importance to the members of a nesting pair, since they must frequently coordinate their movements. An increase in the extent of white tail spotting might render this signal more effective.

Wear.—The primaries, and especially the rectrices of first-year towhees are noticeably more worn than those of adults. Emlen (1936:100) noted this in *Corvus brachyrhynchos* and suggested that wear on the juvenal flight feathers might result in part from the severe treatment which they receive while the young are in the nest, and, possibly more important, from weaker and more brittle construction than that of the adult flight feathers. Wear during the nestling stage does not seem important in the Spotted Towhee, as the remiges and rectrices of two independent juveniles collected on June 8 and July 6 are only very slightly worn. Of great importance, however, is the chronological age of the feathers themselves. In September, when the flight feathers of the adults are fresh, such feathers have been borne for two or three months by first-year birds, and they are already worn to some degree. This differential will, of course, exist between first-year and adult birds until the following fall, when the entire plumage will be replaced by members of both groups.

As Emlen (*loc. cit.*) and Pitelka (1945:255) have pointed out for *Corvus* and *Aphelocoma*, respectively, differential wear is variable and is not a reliable criterion for determining age. However, Emlen found that "the occurrence of heavily worn tail feathers can be linked with first-year birds in a high percentage of cases," and Pitelka used differential wear as a means of spotting first-year Scrub Jays in the field in spring. He also found that specimens with excessively worn flight feathers were almost always first-year birds. The amount of wear on the primaries has been used as a criterion for determining age in other species (*Pipilo fuscus*, Davis, 1951:3–4; *Passerella melodia*, Marshall, 1948:240). As stated previously, differences in wear on and shape of the rectrices can be used effectively in combination to determine the ages of most specimens of the Spotted Towhee. Differential wear is of lesser value during the summer as the feathers of most individuals, regardless of age, are heavily worn by that time. However, extremely worn Spotted Towhees are almost always first-year birds as judged by other characters.

Color of the iris.—The color of the iris is grayish brown in juvenal Spotted Towhees and an intense red in adults. From the fall through the winter and early spring iris color slowly changes in first-year towhees until red irides similar to those of the adults are

acquired. The length of time over which this change takes place is variable, but most first-year birds acquire a fully red iris color by the end of May.

The first change noticeable in the grayish brown iris of the first-year bird is a suffusion of orange or reddish orange proximally, the peripheral portion retaining the juvenal color. After the peripheral portion has changed color, the iris may be pale orange, orange, reddish orange, orange red, or pale red. In a few first-year birds the irides in fall were a dull, brownish red, quite different from the vivid red of the adult iris.

Of 60 males collected between September 14 and May 25, and classed as adults on the basis of plumage and/or skull characters, 58 had red irides and two had pale irides. Of 43 first-year males collected during the same period, 37 had pale irides and six had red irides. Actually the separation might have been even more discriminating than the above figures indicate. When collecting was begun in January, 1955, I was unaware of the limits of variation of the eye color in adults and termed the eye color of all individuals regardless of age "red" unless the iris was unusually pale. As collecting progressed and more adults were examined, it became evident that the eye color of adults varied within very narrow limits and it was then possible to discriminate more accurately between the eye color of adults and first-year birds. Thus, of seven first-year males collected from January through April, 1955, the eye color of four was termed "red." In contrast, of 19 first-year males collected in the corresponding months in 1956, the eye color of only one was termed "red," that of a bird collected on April 25. The usefulness of this character should not be obscured by the initial inability to discriminate more accurately during the period of early collecting.

Of 33 adult females collected between September 14 and May 25, the eye color of all was red. Of 23 first-year females collected in the same period, the eye color of 15 was pale, and in eight it was red. Here again, the value of this character is obscured by the initial lack of familiarity with the nature of variation of the eye color of adults. Of six first-year females collected from January through April, 1955, four were assigned a "red" eye color. In the corresponding period in 1956 only one of ten first-year females was assigned a "red" eye color; this was a bird collected on March 14.

Useful though this character may be, it has obvious limitations. Very few collectors note the eye color of the Spotted Towhees which they take, and this information is lacking for the great majority of museum specimens. Further, as may be judged from what has been written previously, some familiarity with the variability of eye color is required before fine discrimination between age groups can be made. Nonetheless, bird banders could use this character to advantage after handling a number of individuals. It would also be helpful to taxonomists if museum collectors noted the presence of unusually pale eye color in specimens of Spotted Towhees.

The whole problem of iris color is simplified in the western and Mexican races of *Pipilo erythrophthalmus,* since the definitive eye color in all these races is red. The problem would be more complex in dealing with the eastern races, in which the definitive eye color may range from red through pale orange or yellow to straw. Dickinson (1952:332) has pointed out that numerous winter records of the red-eyed, migratory nominate race have been published, based on field observations of iris color. He notes that many of these records may actually pertain to one of the southern races, *P. e. canaster,* in which eye color is variable, ranging from red to pale orange, or even to yellow. Another source of error may be present in such attempts to identify subspecies through eye color alone. It may well be that the eye color of first-year *P. e. erythrophthalmus* passes through a series of orange or reddish orange stages as it changes from the brownish color in juveniles to the definitive red. If this be true, and if the transition takes as long in *erythrophthalmus* as it does in *megalonyx,* many first-year *erythrophthalmus* on the wintering

grounds would have pale irides which might resemble those of one of the southern races. If iris color changes directly from brown to red in first-year *erythrophthalmus*, this would represent a radical departure from the nature of the transition in *megalonyx*, which is probably representative of the western races in this regard.

Bursa Fabricii.—The presence of a bursa Fabricii has long been known as an indicator of age in many species of birds. In the Spotted Towhee this structure is very prominent in juveniles, but it disappears rapidly and in most individuals it is indistinguishable macroscopically by early winter. In the present series, the first male of the year without a visible bursa was collected on December 5, and the first female on January 18. Of four first-year males collected on January 26 and 27, the bursa was not visible in two, and it was present in two, measuring 4.5 and 6 mm. A bursa 3 mm. long was present in a male collected on February 1. Of four first-year males collected on February 4, a visible bursa was present in only one, measuring 2 mm. From this date on, only one first-year male, collected on March 14, had a bursa; this measured 2 mm. In the more limited series of females, a bursa was visible in first-year birds collected through December 5. A female collected on January 18 lacked a bursa and from this date on none was found. It is apparent that the bursa Fabricii is of very limited usefulness in determining age in Spotted Towhees. However, collectors should record the presence of a bursa in birds with ossified skulls, regardless of the date of collection.

SUMMARY

The following characters may be used in combination for determining age in the Spotted Towhee: (1) color of the primary coverts (of particular importance in males); (2) shape of the rectrices; (3) width of the white spot on the fourth rectrix; (4) amount of wear on the wings and tail; and (5) color of the iris.

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Hastings Reservation, Carmel Valley, California, February 10, 1957.

CHARACTERISTICS AND STATUS OF THE SOLITARY SANDPIPER IN UTAH

By RICHARD D. PORTER and JOHN B. BUSHMAN

When Woodbury, Cottam, and Sugden (1949) compiled their check-list of the birds of Utah, only two specimens of the Solitary Sandpiper (*Tringa solitaria*) were known from the state and both were assigned to the race *T. s. cinnamomea*. One (UUMZ 5075), collected on July 9, 1937, two miles southwest of Poncho House, San Juan County, was reported by Woodbury and Russell (1945:48). The other was reported by Twomey (1942:392) and was taken at the Ashley Creek marshes, two miles south of Jensen in Uintah County. This latter has not been examined by us.

Behle and Selander (1952:26–27) reported two additional specimens from Ibapah, Tooele County (UUMZ 10719), and Farmington Bay, Davis County (UUMZ 10984). They also studied the specimen (UUMZ 5075) reported by Woodbury and Russell (*loc. cit.*), as well as a specimen (UUMZ 4142) from Navajo County, Arizona (Woodbury and Russell, *loc. cit.*). All of these were referred to the race *T. s. solitaria*. Since Twomey (*loc. cit.*) had reported that the Ashley Creek birds remained as residents and were paired and doubtless nested, even though the nests were not located, Behle and Selander felt that they too should be referred to *T. s. solitaria*.

Hellmayr and Conover (1948:119–121) give the breeding range of *T. s. cinnamomea* as northern Canada from the tree limit south to about 60° north latitude and from the Bering Sea to the west coast of Hudson Bay. They record the race *T. s. solitaria* as breeding from northern British Columbia, Alberta, Ontario, central Saskatchewan, central Manitoba, and Labrador south to about latitude 50°N. According to them, *T. c. solitaria* migrates primarily east of the Mississippi River while *T. s. cinnamomea* migrates principally west of the Mississippi River. Both subspecies winter in South America.

We wish to thank William H. Behle, William B. Davis and Keith L. Dixon for their helpful criticisms of this manuscript. We are also grateful to Gorman M. Bond for verifying several of the specimens discussed here.

The collection of six additional Solitary Sandpipers by us from Skull Valley in Tooele County in August and September of 1954 brings the total number of known specimens for the state to ten. A study of these re-opened the question of the status of the two races in Utah and led to a re-evaluation of the previously reported specimens. Table 1 summarizes the characteristics of these ten specimens. Only one of these six specimens conforms to *T. s. solitaria* in every character. Its identity has been corroborated at the United States National Museum by G. M. Bond. The spots on the dorsum of all of the remaining five birds are buffy in coloration, while the background color is an olive-brown. Conover (1944:543) states that the buffy dorsal spots are the most distinctive feature of immature birds of *T. s. cinnamomea*. According to him, they are a very constant character at least through September and wherever found serve to identify the individual as *T. s. cinnamomea*. He likewise considers an olive-brown background color between these spots as being typical of immature birds of that race. The wings of four of the five specimens all fall within the range of measurements for *T. s. cinnamomea,* as given by Conover. The wings of the fifth specimen (sex unknown) fall only one-tenth of a millimeter short of the range of male *T. s. cinnamomea,* but fall well within the range of either male or female *T. s. solitaria*. Since it is typical of *T. s. cinnamomea* in most other respects it is referred to that race.

The inner web of the outermost primary of three of the six specimens shows degrees of spotting or white vermiculations from faintly mottled to plainly marked. Taverner (1940:215) considers the presence of these vermiculations as definite evi-

dence that a specimen carrying them is of the race *T. s. cinnamomea,* while Conover (*loc. cit.*) considers the presence of vermiculations as almost conclusive evidence that an immature bird exhibiting this character is of the race *T. s. cinnamomea.* Conversely, the presence of immaculate outer primaries, according to them, does not necessarily indicate that the specimen is *T. s. solitaria.* Of the two remaining specimens, both of which have immaculate outer primaries, one is typical of *T. s. cinnamomea* in all other respects. Consequently it is referred to that race. The other, which seems to be somewhat intermediate between the two races, more closely approaches *T. s. cinnamomea.*

Thus, of the six specimens recently collected, one is definitely referable to *T. s. solitaria* and three to *T. s. cinnamomea.* The two remaining specimens show one or more characters that appear to be intermediate between the two races, but they are referred to *T. s. cinnamomea* because they have a greater number of characters of *T. s. cinnamomea.*

We feel that three of the specimens previously reported from the state are of the race *T. s. cinnamomea.* The fourth (UUMZ 10984), which has dark upper parts heavily spotted with considerable amounts of white and some buff, appears to be somewhat intermediate, but probably is also referable to *T. s. cinnamomea* on the basis of wing length and the faint white mottling on the outer primary (see table 1). Although Behle and Selander (1952:26) reported specimen UUMZ 10719 as having immaculate primaries, the outermost primaries appear to us to be slightly mottled with white (table 1).

Part of the confusion of the identity of the previously reported specimens arises from the fact that at least two of them were presumed to be breeding birds. However, it is doubtful that the species breeds in the state. Behle and Selander (*op. cit.*) considered the Ibapah specimen (UUMZ 10719), which was collected by Porter on July 15, 1950, to be a breeding bird because it had enlarged testes (12 mm.). However, Porter's field notes state that the testes of this bird measured only 2 mm. in length, which eliminates the likelihood of its breeding at Ibapah. This confusion as to the size of the testes unfortunately resulted from the way in which the data were written on the tag.

Concerning the Uinta Basin birds, Twomey (1942:392) reports that A. C. Lloyd, while at Ashley Creek marshes, saw four or five of these sandpipers almost every day in 1934 and 1935. Twomey states that at least two pairs remained as residents in 1937. He also indicates that, although no nest was found, they were paired and no doubt nested. Twomey (*op. cit.*) does not state whether the one bird he collected at the Ashley Creek marshes was a breeding bird or a migrant, as he gives no indication of the date it was collected nor the condition of its gonads. In their check-list of the birds of Utah, Woodbury, Cottam, and Sugden (1949:13) record only the race *T. s. cinnamomea* and list it as a casual summer resident breeding in Uintah and Kane counties, perhaps elsewhere, and a sparse migrant throughout the state. Behle and Selander (*loc. cit.*) found the two Kane County specimens to be Spotted Sandpipers (*Actitis macularia*) in winter plumage. These two specimens are probably the same birds referred to by Woodbury and Russell (1945:48) as breeding at 8500 feet on Cedar Mountain, Iron County, 100 miles northwest of the Navajo Mountain.

Thus, it appears that the Solitary Sandpiper probably does not breed in Utah in either Tooele (Ibapah) or Kane counties. It seems unlikely that they should breed this far south of their usual breeding range in Canada (about 50° north latitude, Conover, 1944:538), in spite of the fact that Twomey (1942:392) reported seeing these birds in Uintah County in the summer and believed that they probably nested. It appears more likely that the birds reported by Twomey were either stragglers or late spring or early summer migrants. Records from Utah (table 1) indicate that the Solitary Sandpiper, like many other species of sandpipers, is an early summer migrant. This is substantiated by Bent (1929:11–15) who reports records in July in many areas throughout the coun-

try. In addition, as the name implies, these sandpipers are usually found singly, in pairs, or in small flocks of three or four, which could very well give the impression that they were mated and nesting. Another factor against the likelihood of this species nesting in Utah is that all of the specimens studied by us that were collected in the state in the course of the nesting season seem to be representatives of the more northern subspecies, *T. s. cinnamomea,* whereas if they had been breeding birds, they probably would have belonged to the southern race *T. s. solitaria*. Until a nest of this species is actually found in Utah it seems preferable to consider this species as a migrant and an occasional summer straggler rather than a nesting species. The latest known date for Utah during fall migration for this species is an observation made by the authors on September 22, 1954, at Orr's Ranch, Skull Valley, Tooele County.

Table 1

Summary of Characteristics of Solitary Sandpipers from Utah in terms of Diagnostic Characters of races given by Conover (1944)

UUMZ No.	4142	10719	10984	13747	5075	13746	13844	13845	13846	13748
Sex	♂	♂	♂	♂	♀ ?	♀	♀ ?	♀	......	♀ ?
Wing length	135.6	130.0	132.9	129.0	142.6	137.5	129.3	137.6	127.9	119.6
sol.		x		x			x		x	x
cinn.	x	x	x	x	x	x	x	x		
Outer primary										
sol.				4				4		4
cinn.	2	2	3		1	2	1		3	
Dorsal color and spotting										
sol.			x							x
cinn.	x	x		x	x	x	x	x	x	
Loral and supraloral										
sol.				x		x	x		x	x
cinn.	x	x	x		x			x	x	
Cheek and throat										
sol.				x		x	x	x		x
cinn.	x	x	x	x	x	x	x	x	x	
Weight in grams	....	....	....	49.3	....	62.1	47.3	59.3	53.2	41.3
Date collected	July 14–37	July 15–50	June 10–50	Aug. 12–54	July 9–37	Aug. 9–54	Aug. 31–54	Sept. 13–54	Aug. 17–54	Aug. 12–54
Determination	cinn.	cinn.	cinn. ±sol.	cinn. ±sol.	cinn.	cinn.	cinn.	cinn.	cinn.	sol.

x indicates character present normal for race shown; 1, inner web of outer primary plainly mottled with white vermiculations; 2, inner web slightly mottled; 3, inner web faintly mottled; 4, immaculate outer primary.

In summary, the race *T. s. solitaria* of the Solitary Sandpiper is known in the fall from only one specimen collected in Skull Valley, Tooele County, on August 12, 1954. The race *T. s. cinnamomea* is known in the spring from only one specimen collected on May 10, 1950 (Behle and Selander, 1952:27) and in the summer and fall from as early as July 9 until September 13 (see table 1).

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FROM FIELD AND STUDY

The Display of the Sickle-billed Bird of Paradise.—Crandall (Zoologica, 11, 1932:82–84; 31, 1946:9) has described the display of captive specimens of the eastern New Guinea Long-tailed Bird of Paradise (*Epimachus meyeri meyeri*). Few people have watched this species or its relative *Epimachus fastosus* in the wild state. In March, 1938, I was camped at 5200 feet on Mount Kourangen in the Tamrau Range which runs from east to west along the northern coast of the Vogelkop of Netherlands New Guinea. In the course of two and a half weeks on the mountain, we collected several specimens of the Sickle-bill (*E. f. fastosus*), but only twice did I manage to have any detailed view of the birds. At this season other species of Birds of Paradise were displaying on their display posts, but, at the time, thinking only of the display in a restricted cage described by Crandall (*loc. cit.*) for *Epimachus,* it had not occurred to me that I was watching a type of display when I witnessed the following activity of a Sickle-bill (notes of March 20):

"A male was sitting very high up on the bare branch of a huge dammar, *Agathis* sp., in a display posture. The pectoral shields were spread out and upwards like two raised arms. The tail was partially spread showing the shorter, outer feathers. A brownish bird, presumably a female, was sitting near on a lower branch. Suddenly the male called, a loud penetrating whistle sounding like the syllable 'whick.' Then, so rapidly that I could not see the pectoral shields retracted, he turned and dived straight downwards off the branch towards the ground, perhaps a hundred feet below."

From my position on the steep hillside partly above the base of the dammar, it was impossible to estimate the exact distance from the ground when the bird concluded its maneuver, but it must have been only a few feet from the bushes at the base of the tree.

"At the bottom of the dive, the male came out with spread wings and sailed back up again to the same branch almost as if on the rebound, so rapidly that it took me an instant to realize anything had happened at all."

In retrospect, this striking performance, which I witnessed only once, seems undoubtedly to have been a type of display. Its pattern bears an interesting resemblance to the display flight of the Anna Hummingbird (*Calypte anna*) so well described by Woods (*in* Bent, Bull. U. S. Nat. Mus., 176, 1940: 371–2).—S. Dillon Ripley, *Peabody Museum, Yale University, New Haven, Connecticut, January 21, 1957.*

The Classification of the Oscine Passeriformes.—Any arrangement of the family groups among perching birds is subject in some part to individual conviction, since it is obvious that to compress what is definitely a three-dimensional relationship into a linear sequence on the printed page requires occasional arbitrary decision as to the order among families that are closely related. However, the general framework should be based on characters that point to the basic standing of the various groups. This is particularly true of the assemblage that is to stand at the head of the list, assuming that this position is to be assigned to those birds that are believed to have advanced to the greatest degree in their general evolution from their ancestral stock.

Current acceptance of the position of the nine-primaried fringilline assemblage at the head of the list has been general in recent years, although with differences of opinion as to the family limitations within this group. My own opinions on the matter are covered in the classification that I have proposed (Smiths. Misc. Coll., 117, No. 4, 1951:12, 21–22) in which the orders have followed rather closely those of Gadow, with changes due to more modern information, while the family limitations have been considerably modified.

Mayr and Greenway (Mus. Comp. Zool., Breviora, 58, 1956:1–11) recently have published an outline classification of Passeriformes which it is proposed to follow in the final volumes of the Check-list of Birds of the World, begun by James L. Peters. In this they return again to the procedure used generally by the previous generation of ornithologists, in which the Corvidae are placed at the end. In this I believe that certain basic data either have been overlooked or have not been accorded sufficient weight.

The position of the Corvidae relative to the other families is a matter that has intrigued me from my earliest studies in this field. In the beginning it seemed reasonable to accept the prominent position

usually accorded them, because of the outstanding size found in the genus *Corvus* that gives the family its name, and also the strong learning ability that corvids possess.

Consideration of passeriform classification led me to careful examination of the skeleton, and I observed differences in the form of the head of the humerus (fig. 1) that offered aid in family arrangement. In the Corvidae, the internal tuberosity, separated from the rounded articular head by the broad capital groove, overhangs the pneumatic fossa from which the rather large foramen leads into the hollow shaft. This is illustrated in figure 1*a*, which shows the upper part of the humerus in the American Crow (*Corvus brachyrhynchos*).

Among major groups of nine-primaried Oscines, such as the Fringillidae, Thraupidae, and Icteridae, on the other hand, this internal tuberosity has a bladelike form, while the fossa from which the foramen opens is enlarged so that it extends back beneath the base of the head. The tuberosity, while varying somewhat in different species, is included in the lateral boundary of the fossa as an irregular projection on its anterior wall, and tends to divide the concavity into two irregular parts. The narrowed blade thus becomes decidedly more prominent, as illustrated in the Cardinal (*Richmondena cardinalis*) shown in figure 1*c*.

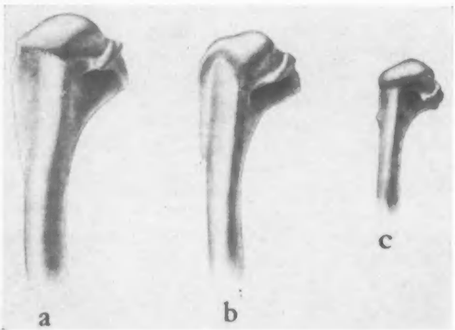

Fig. 1. *a*, upper part of the humerus of American Crow (*Corvus brachyrhynchos*); *b*, Pileated Woodpecker (*Dryocopus pileatus*); *c*, Cardinal (*Richmondena cardinalis*).

Curiously enough in these early studies it became evident at once that the resemblance of the Corvidae in this regard was with the Tyrannidae and their allies, and these are universally considered as low in the passeriform order. And further, it was seen that the Corvidae resemble also the Piciformes, illustrated in the Pileated Woodpecker (*Dryocopus pileatus*) shown in figure 1*b*. In fact, this style of formation of the humeral head, sometimes in slightly modified form, continues through the Coraciiformes, Trogoniformes, and other adjacent orders.

The form of the head of the humerus is not subject to stresses which might cause modification with any of the usual changes in type of food, habit, or habitat that appear to have affected the form of such structures as the bill and the feet, with their supporting bony framework. It remains the same in related groups, regardless of whether the method of flight is strong and direct, like that of a grackle, or weaker and undulating, like that of the cardinal already mentioned. The meadowlark, which alternately flits the wings rapidly and sails, resembles its relative the grackle. Even the swifts, highly modified for rapid flight, show no marked departure from related groups in this portion of the humerus. It must be evident, therefore, that there is here a character of phylogenetic significance, of value in judging close relationship, and useful as a detail in arranging the levels of classification. It has been this close resemblance of the Corvidae to groups that all admit stand low that has led me to join Ridgway and some others in deposing the crows and their allies from the lead position that they long had occupied and to place them near the beginning of the oscinine families.

The Fringillidae and related families at the same time have been elevated to the higher level.

Repeated consideration of these matters in expanding studies over a period of nearly 40 years has sustained fully my early opinions. To place the Corvidae at the highest level on the basis of greater mental capacity is to ignore these actual facts.—ALEXANDER WETMORE, *Smithsonian Institution, Washington, D.C., January 15, 1957.*

Unusual Early Winter Records from Oregon.—In 1953 and 1955, field work in connection with distributional studies being carried on for the United States Fish and Wildlife Service took me into Oregon for a brief interval in late November and December. My activities then were concerned largely with migratory game species, but notes were kept of other birds observed while in the field, and an occasional specimen was taken to verify unusual occurrences. Among the latter, the following seem of sufficient interest to justify placing on record at this time. In each instance subspecific determination was made by John W. Aldrich.

Regulus calendula cineraceus. Ruby-crowned Kinglet. At Pendleton, on December 12, 1953, a male was collected as it fed with a flock of Black-capped Chickadees (*Parus atricapillus*) in woods bordering the Umatilla River. Gabrielson and Jewett (Birds of Oregon, 1940) consider this species rare in winter in eastern Oregon and state that only *Regulus calendula grinnelli* has been taken east of the mountains at this time of year. It is of interest, therefore, that this specimen was found to represent the race *cineraceus.*

Dendroica townsendi. Townsend Warbler. Rather unexpected was the presence of a female Townsend Warbler at Pendleton on December 12, 1953, where it was feeding with the previously mentioned flock of Black-capped Chickadees in woods bordering the Umatilla River. Gabrielson and Jewett list but three winter records for the state, all for the Portland area; this is apparently the first record at this season of the year for eastern Oregon.

Wilsonia pusilla pileolata. Pileolated Warbler. At Coquille, 17 miles south of Coos Bay, a female Pileolated Warbler, representing the race *pileolata,* was collected on December 6, 1955, as it fed alone in underbrush fringing a small stream. This would appear to be not only the first winter record of this race for Oregon, but also the first record for its occurrence in the western part of the state. Gabrielson and Jewett give the status of *pileolata* in Oregon as a fairly common summer resident east of the Cascades, with extreme dates of occurrence as April 29 and September 21.

Melospiza lincolnii gracilis. Lincoln Sparrow. Although considered by Gabrielson and Jewett (*op. cit.*) as an uncommon migrant in the state, the presence of *gracilis* in western Oregon in December suggests the possibility that the Lincoln Sparrow winters in at least small numbers. At Coos Bay on December 7, 1955, three individuals were noted feeding with Song Sparrows in alders bordering a stretch of open marsh and a male that was collected was found to be typical of this northern coastal race.

Melospiza georgiana ericrypta. Swamp Sparrow. At Tillamook, on November 29, 1955, a female Swamp Sparrow, representing the race *ericrypta,* was collected as it fed with other sparrows in alders bordering a large open marsh. As far as now known this is the first record for the occurrence of this species in Oregon.—THOMAS D. BURLEIGH, *Fish and Wildlife Service, Moscow, Idaho, January 14, 1957.*

Migratory Flight of a Zonotrichia at 10,000 Feet Above Ground Level.—On October 31, 1956, Mr. Francis Drake was flying a single-engine Beech Bonanza airplane from Sacramento to San Bernardino, California. Between 9:00 and 9:15 p.m. while following a Civil Aeronautics flight plan at 10,000 feet above sea level, he felt a dull thud in the forward part of the plane. On landing at San Bernardino he inspected the front of the plane and found a dent at the right border of the air vent. Part of a bird was lodged in the air intake and this was retrieved for identification. It proved to be the foot, tarsus, and lower shank of a sparrow of the genus *Zonotrichia.* I am much indebted to Marshall G. Richardson and J. Stuart Rowley, as well as to Mr. Drake, for supplying information about this incident and for forwarding the specimen for examination.

The foot and lower leg feathering match in all details of size, color, and structure those of a Golden-crowned Sparrow (*Zonotrichia coronata*). The tarsus and foot are too large for *Zonotrichia leucophrys.* However, the Harris Sparrow (*Zonotrichia querula*), which reaches California in small numbers, cannot be distinguished on the basis of these parts from the Golden-crowned Sparrow. But

the probabilities are very strong that the remains are those of the Golden-crown, and certainly they represent one or the other of the two large species of *Zonotrichia*.

When the bird was struck, the plane was between Tulare and Delano in the San Joaquin Valley, and since the ground there is but 300 feet above sea level, the bird must have been flying approximately 10,000 feet above the surface. A northwest wind of 40 miles per hour was blowing at 10,000 feet at the time. Accordingly, the bird, with an air speed capacity of about 30 miles per hour, could have made little headway in a westerly direction. This minimizes the possibility that it had been forced to high elevations by recent crossing of the Sierran crest to the eastward and had continued on in a westward direction. The locality where it hit the plane is in any event about 40 miles west of elevations of 5000 feet in the Sierra Nevada and about 70 miles west of the Sierran passes that are 10,000 to 12,000 feet. If the bird came from the west, it would have had to cross the ridges of the inner coast ranges, but these usually do not exceed 4000 feet and are some 70 miles distant. Thus, there is little reason to suppose that this sparrow had recently been forced to this height by the necessity of crossing mountain systems. If this had happened earlier in its flight, it would have occurred before dark and in the high Sierra, a region rarely if ever visited by the large species of *Zonotrichia*. The probabilities are much greater that the bird was travelling along the axis of the broad plain of the Central Valley of California in southward migration, riding a northwest wind, and that the height above ground was attained without the influence of mountains.

The consensus of recent students of migration is that most movements of passerine birds, while little influenced by actual elevation above sea level, are carried on within 3000 feet of the ground (see for example Wing, Nat. Hist. Birds, 1956:104). Lowery (Univ. Kansas Publ. Mus. Nat. Hist., 3, 1951: 389) in his calculations used for recording numbers of nocturnal migrants seen passing across the face of the moon assumes a ceiling for flight of one mile above the ground. The present occurrence seems to suggest that occasionally, although doubtless rarely, flight may reach greater heights uninfluenced by the nearness of mountainous terrain.—ALDEN H. MILLER, *Museum of Vertebrate Zoology, Berkeley, California, December 30, 1956.*

Specimen of Parula Warbler from Southern California.—On April 29, 1956, in the course of a field trip to Thousand Palms Oasis, 11 miles east of Palm Springs, Riverside County, California, I observed a Parula Warbler (*Parula americana*). It was collected by Ross Hardy and proved to be a male. The testes were small (2 mm.) and it was not fat. Frank A. Pitelka, after examination of the specimen, points out that there is reason to believe that it is a first-year bird because of the small size (wing 54.8, tail 37.5) and the worn, faded condition of the remiges and rectrices. The bird was in tamarisk trees along a small stream in a migrating flock of birds composed of yellow (*Dendroica aestiva*), Audubon (*D. auduboni*), Townsend (*D. townsendi*), Tolmie (*Oporornis tolmiei*), and Pileolated (*Wilsonia pusilla*) warblers. So far as could be determined there was but the one individual of this species. The specimen is now number 134973 in the Museum of Vertebrate Zoology.

So far as the writer can determine, the Parula Warbler has not been recorded from California. Its normal distribution is in the Mississippi Valley and areas to the east and north.

I wish to thank Frank A. Pitelka and Don R. Medina for examination of the specimen and M. Dale Arvey for assistance in preparation of this report.—PATRICK J. GOULD, *Moore Laboratory of Zoology, Occidental College, Los Angeles, California, December 31, 1956.*

Two Records of Unprovoked Attack by Golden Eagles.—Arnold (The Golden Eagle and its economic status, Fish and Wildlife Serv. Circ. 27, 1954:3–4) cites and discounts three alleged unprovoked attacks by Golden Eagles (*Aquila chrysaëtos*) upon humans and cites another attack (Ridgway, The Ornithology of Illinois, Part 1, 1889:484) which was provoked by disturbing two feeding eagles. On two occasions while performing naturalist duties in Mount Rainier National Park, Washington, I was subjected to unprovoked attack by immature Golden Eagles.

The first attack came late in the afternoon of July 23, 1947, just as I emerged from a dense thicket of firs and pines at timberline onto a barren, rocky ridge on the northeast slope of Mount Fremont, about 2 miles northwest of the Yakima Park headquarters. The first warning I had of this attack was a sound like the whine of a bullet fired from a high-powered rifle, and my reaction was to 'hit the dirt.' Even though I was flat on the ground, the bird passed close enough to ruffle my hair. Having missed

on its first pass, the eagle gave a piercing *kreeee* scream and began circling and climbing for altitude. When it reached a height of several hundred feet, it folded its wings and stooped again. This time a rock thrown while it was still some distance above me caused the eagle to veer off. It indicated no further interest in my presence and left the area. I learned later that another Park Service employee had been subjected to a similar attack in the same area a week earlier.

A year later, on the morning of August 16, another young Golden Eagle made repeated attacks on me as I walked over a tableland known as Grand Park, about 2 miles northwest of where the incident of 1947 occurred. Again, I had just emerged from a heavy conifer forest onto a barren, exposed ridge when this bird left its companion about a mile away and flew over to investigate my presence. The eagle attacked immediately and repeatedly from an altitude of about 50 feet, making perhaps a dozen dives within a 2- or 3-minute period. After either having satisfied its curiosity or become dissatisfied with its inability to take this prey, the eagle returned to its companion. However, in the next three hours one of the two birds made about ten separate attacks on me, each time having to make a flight of a mile or more from where they were foraging.

The attack made in 1947 and the initial attack made in 1948 both seemed to represent instances of misidentification of prey by young, inexperienced Golden Eagles. Neither of these attacks could be accounted for on the grounds of nest defense or the defense of killed prey. These areas were seldom frequented by humans, and the native fauna apparently reacted to man, upon encountering him, largely in accordance with the relative sizes and habits of the animals involved. To eagles soaring high above the ground, the upright stature of man gives little evidence of size, and from the overhead point of view a man has no more breadth nor width than the hoary marmot (*Marmota caligata*), a species much preyed upon by Golden Eagles. Both initial attacks seemed to have been earnest attempts to take an unfamiliar but fairly small animal.—Gordon W. Gullion, *Austin, Nevada, December 19, 1956.*

Acadian Flycatcher, a New Bird for British Columbia.—For over twenty years there has been in the bird collection of the Carnegie Museum an unrecorded specimen of the so-called Acadian Flycatcher (*Empidonax virescens*) from British Columbia—an area far beyond the recognized range of the species. The bird was collected at Leonie Lake (3200 feet), near Barriere, Cariboo District, by George M. Sutton, on June 9, 1934. The collector noted that the testes were much enlarged. The occurrence of this flycatcher so far west and north is of course purely accidental.—W. E. Clyde Todd, *Carnegie Museum, Pittsburgh, Pennsylvania, January 4, 1957.*

A Second Record of the Yellow-bellied Sapsucker from St. Croix, Virgin Islands.—Sapsuckers are rare winter visitants in the Virgin Islands. Nichols (Memorias de la Sociedad Cubana de Historia Natural, 17, 1943:23–27) reports *Sphyrapicus varius* as occasionally seen on St. Thomas in the Virgin Islands, and Seaman (Wilson Bulletin, 66, 1954:61) collected a female on January 24, 1950, on Anegada. The only Sapsucker hitherto collected or reported in St. Croix was a female of *S. varius varius,* shot on January 3, 1924, on Estate La Grange (Beatty, Jour. Dept. Agr. Puerto Rico, 14, 1930:135–150).

About a year ago I bought a part of Estate Bellevue, on St. Croix, which included an area of about an acre on which the small tree *Bourreria succulenta* is common. The smooth bark of nearly every one of these trees is well marked by unmistakable Sapsucker workings, and some of them have been very extensively perforated. A single one of the many West Indian mahogany trees (*Swietenia mahagani*) in the area also shows a few Sapsucker workings, but trees of *Exostema caribaeum* (yellow torch), *Bursera simaruba* (turpentine), *Albizzia lebbeck* (woman's tongue), and *Torrubia fragrans* (black mampu) are untouched. From the changes in the appearance of these workings since I first found them it appears that they were made in the winter of 1954–55.

Mr. Albert Powell, of Nevis, tells me that on November 27, 1956, a Sapsucker was present and spent about two hours, mostly on one *Bourreria*. Powell had never before seen a woodpecker and was much impressed by its ability to hitch down the tree as well as up, and by its method of tearing off and casting aside shreds of bark that got in its way. He reports that after the Sapsucker left, its workings were visited by Bananaquits (*Coereba flaveola*) and lizards (*Anolis cristatellus*). Fresh

workings were also found on other *Bourrerias* that were not made while Powell was there, so the bird had been present more than once.—R. M. BOND, *Kingshill, St. Croix, U. S. Virgin Islands, December 3, 1956.*

A Further Observation on Torpidity in the Poor-will.—Few instances of torpidity in wild Poor-wills (*Phalaenoptilus nuttallii*) have been reported (see Marshall, Condor, 57, 1955:134). Thus it seems desirable to set forth information on a torpid individual found in the Berkeley Hills in Tilden Regional Park, Contra Costa County, California.

On March 11, 1956, at 4:00 p.m. I flushed a Poor-will from a hillside in Big Springs Canyon. On the 14th, at 10:50 a.m., what may have been the same individual was found at the same place basking in full sunlight on a small platform of earth at the entrance to a gopher burrow. I had excavated the burrow on March 9 in an attempt to capture a lizard that had taken refuge there. The enlarged opening was of adequate size to accommodate the bird and was probably the place from which the Poor-will had been flushed three days before. The bird had its back to the sun, the long axis of its body in line with the sun's rays. Its eyes were closed and its wings slightly extended. At 11:45 a.m., nearly an hour later, I returned in expectation of obtaining a motion picture of the bird in the act of leaving the burrow and found it had moved some eight inches forward into the hole. Only its tail and a portion of one wing were still in the sun. As I photographed the Poor-will, my wife probed it several times with her finger, attempting to cause it to take flight. Failing in this, she took it in hand and discovered that it was inert, although it hissed briefly when first seized. She placed it on the ground but it did not fly.

After a few minutes the bird was returned to the hole. Once again it hissed, this time more strongly than before. In a few minutes it was removed again and placed on a rock in the sun where it rested quietly, showing no sign of life. As my wife attempted to pick it up again, it opened its mouth. In order to get additional pictures of the mouth movements, the bird's throat was tapped repeatedly. This stimulated it to open its eyes and mouth several times. The bird was then returned to the hole while I changed the position of the camera. When placed on the ground again, it fluffed out its feathers, extended its wings slightly, and once more opened its eyes briefly. It was picked up and placed on the rock in the sun and its throat probed to elicit the mouth movements. It responded by opening its mouth once, but it would not do so again. It then took flight, over 15 minutes having elapsed since it was first touched.

The burrow was checked on subsequent days but the bird was not found. However, on October 16, 1956, at 9:15 a.m., a Poor-will was flushed within 30 feet of the same burrow. This individual (possibly the same bird) was fully alert, taking flight when I was at a distance of 15 feet. It made a single cat-like meowing note as it left the ground. It had been sitting in a small depression among rocks at the base of a clump of California sagebrush in mixed light and shade.

The site of these observations was on the crest of a gentle knoll on the south-facing slope of Big Springs Canyon, about 50 yards up slope from the canyon bottom. The angle of the slope is about 30°. The substratum consists of mixed soil and small rocks, with patches of open bare soil interspersed with grass. There are scattered clumps of California sagebrush (*Artemisia californica*), coyote bush (*Baccharis pilularis*), and sticky monkey flower (*Diplacus aurantiacus*). A group of conifers borders a fire road some 30 feet up slope. The area is fully illuminated all day and is somewhat sheltered from wind by the conifers and a willow thicket. It is one of the warmest slopes in the area.

The alertness of the bird when it was flushed in the late afternoon on March 11 and the torpidity of presumably the same individual in the morning on March 14 suggest the possibility that it was foraging in the evening and returning to the hole with falling temperatures in the course of the night; torpor then followed and persisted into the next day until eliminated by rising temperatures. It is of interest that in the period of basking the bird had moved into the hole and yet seemed incapable of activity when first handled.—ROBERT C. STEBBINS, *Museum of Vertebrate Zoology, Berkeley, California, November 8, 1956.*

Rough-winged Swallows of the race stuarti in Chiapas and British Honduras.—On September 13 and 15, 1952, a short distance from Tuxtla Gutiérrez, Chiapas, México, and on September 20 at Ocozocoautla, about 30 kilometers west of Tuxtla Gutiérrez, single specimens of Rough-winged

Swallows (*Stelgidopteryx ruficollis*) were collected from flocks feeding over fields. The three birds are of the race *stuarti,* which is similar to, but considerably darker than, *S. r. ridgwayi* of the Yucatán Peninsula. *S. r. stuarti* does not seem to have been recorded heretofore from Chiapas. However, it was to be expected there since it breeds in Alta Vera Paz, Guatemala, the type area, and has been found wintering in Veracruz (Motzorongo, February 11 and 15; M.C.Z. nos. 233622–3), in Tabasco (Brodkorb, Misc. Publ. Univ. Mich. Mus. Zool. No. 55, 1943:70) and on the Yucatán Peninsula (Paynter, Peabody Mus. Bull., 9, 1955:210). The specimens displayed no signs of breeding. All were molting.

In the summer of 1954, at El Real, a ranch 40 kilometers east of Ocosingo, Chiapas, several samples of Rough-winged Swallows were taken from the large flocks which appeared over the pastures each evening. On July 12 seven specimens were obtained, six of which were adults in early stages of molt and which exhibited no indications of breeding; the seventh was a juvenile. The birds are referable to *S. r. fulvipennis,* the resident race of Chiapas (Brodkorb, Condor, 44, 1942:216). Previously I believed *S. r. fulvipennis* to be doubtfully distinct from *S. r. serripennis* (Paynter, *op. cit.*: 209), but since that time I have examined larger series of the species and find that the rufous chin (an approach toward the rufous-throated races farther south), the dark shafts of the under tail coverts, and the darker spotting of the crissum are good characters distinguishing *S. r. fulvipennis* from *S. r. serripennis,* as noted by Brodkorb (*loc. cit.*).

Between August 22 and 25, again at El Real, 25 additional swallows were collected at random from the flocks about the fields. Thirteen proved to be *S. r. fulvipennis* and twelve were *S. r. stuarti.* Both subspecies were in well-advanced molt.

From these data it appears that *S. r. stuarti* occurs in Chiapas as a migrant, or visitant, arriving sometime between mid-July and the third week in August. Molt appears to take place either after the birds have reached their winter quarters or while they are en route, which agrees with Dwight's observations on *S. r. serripennis* (Annals N. Y. Acad. Sci., 13, 1900:230).

In the Museum of Comparative Zoology there are two specimens of Rough-winged Swallows which were collected at Augustine, Cayo District, British Honduras, on April 23 and 25, 1928. These were identified by Austin (Bull. Mus. Comp. Zool., 69, 1929:384) as *S. r. ridgwayi,* although he mentioned that one bird was atypical, in that it had an unmarked crissum. The birds were said to be taken from a small colony which was thought to be nesting in a cavern. Examination of these birds indicates that one, a female, collected on April 23, is typical of *S. r. stuarti,* a subspecies not previously known from British Honduras, while the other, a male taken on April 25, is a good example of *S. r. serripennis.* Unfortunately, the labels bear no notations relative to the condition of the gonads of the specimens, but it would seem that the female was one of the flock thought to be breeding and that the male was a visitant or migrant. April 25 is rather late for *S. r. serripennis* to be so far south, but there are records from Chiapas even as late as May 3 (Brodkorb, *op. cit.*:215).—Raymond A. Paynter, Jr., *Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, November 9, 1956.*

Birds Mobbing a Snake Skin.—Mobbing behavior of birds, especially that directed toward avian predators, has frequently been reported. Less common are reports of birds mobbing non-avian predators or remains of them.

On July 14, 1956, two and one-half miles north of Orinda, Contra Costa County, California, I observed a group of about 20 birds which were obviously excited about something on or near the ground. Four species were present: Spotted Towhee (*Pipilo maculatus*), both adults and young, Wren-tit (*Chamaea fasciata*), Bewick Wren (*Thryomanes bewickii*), and Plain Titmouse (*Parus inornatus*). All were scolding, but the wrens and titmice were by far the loudest. The birds moved rapidly about in a small patch of brush, approximately four feet from the ground, occasionally diving at an object below them. On my approach most of them flew, but two Bewick Wrens remained active until I was within a few feet. From this new position I could see that they were diving at something on the ground. They were directing their attention to a shed skin of a large snake, partly exposed and partly extending into a hole beneath a stump. The skin was later identified by James D. Anderson as that of a rattlesnake, *Crotalus viridis.*—Richard C. Banks, *Museum of Vertebrate Zoology, Berkeley, California, February 2, 1957.*

NOTES AND NEWS

The Editors of the Condor belatedly acknowledge on behalf of the Society the contribution of C. G. Willis which made possible the publication of Don R. Eckelberry's painting in color of Nicaraguan Antbirds in the last issue.

COOPER SOCIETY MEETINGS

SOUTHERN DIVISION

NOVEMBER.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on November 27, 1956, at the Los Angeles County Museum. The following names were proposed for membership: James R. Beer, Dept. of Entomology and Economic Zoology, Univ. Minnesota, St. Paul 1, Minn., Alan H. Penberthy, 21 Rutland Rd., Freeport, N.Y., and William Owel Lewis, Box 22, Ivy, Va., by C. V. Duff; Goran Laestadius, 939 W. 21st St., Los Angeles 7, Calif., Benjamin David Parmeter, Laguna Honda Home, San Francisco, Calif., and Roger W. Williams, A/1C, 333 S. Alvernon Way, Apt. 48, Tucson, Ariz., by Jack C. von Bloeker, Jr.; and Daniel Charles Wilhoft, 2320 Haste St., Berkeley, Calif., by James D. Anderson.

President von Bloeker appointed Ed N. Harrison, W. J. Sheffler and C. V. Duff (chairman) to serve on the Nominating Committee for officers.

Kenneth Stager reported that the C. J. Parkers had observed 75 or more starlings in the Lucerne Valley within the past two weeks. John Tramontano reported that there was a starling in the vicinity of the Audubon Center at this time and that one had been seen there last winter.

Tom J. Cade of the University of California at Los Angeles reported on "Birds of Colville River, Alaska." His talk was illustrated with colored motion pictures.—DOROTHY E. GRONER, *Secretary.*

JANUARY.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on January 29, 1957, at the Los Angeles County Museum. The names of 28 applicants for membership were read, as follows: Henry Washburn, 1013 Walnut Ave., Santa Cruz, Calif., proposed by Charles H. Anderson; Arthur C. Felt, 617 N. Newlin Ave., Whittier, Calif., and David A. Walsh, Box 223, College, Alaska, by Francis H. Boynton; Albert E. Allin, 404 S. Norah St., Fort William, Ontario, Canada, Carrie Avent, Minter City, Miss., D. A. Boag, "Kilmagar," Volmer P. O., Alberta, Canada, Robert P. Breitenbach, Univ. Wisconsin at Milwaukee, 3203 N. Downer Ave., Milwaukee 11, Wis., Jerauld C. Cannon, 233 E. Delano, Tucson, Ariz., Alex Dzubin, Canadian Wildlife Service, 317 Field Husbandry Bldg., Univ. Saskatchewan, Saskatoon, Saskatchewan, Canada, Margaret R. Harding, 526 S. Van Ness Ave., Santa Ana, Calif., D. Elmer Joshson, Box 334, Dugway, Utah, Lotus S. Miller, 529 E. Ninth St., Davis, Calif., Charles H. Richardson, 813 Ashley Rd., Santa Barbara, Calif., Charles T. Stone, Jr., 4514 Ave. N. ½, Galveston, Tex., John W. Terborgh, 4582 26th St. North, Arlington 7, Va., James H. Turner, Box 691, Holloman Air Force Base, New Mex., Allen E. Valentine, 2335 Walter Rd., Westlake, Ohio, George E. Watson, III, Osborn Zoological Lab., Yale Univ., New Haven, Conn., and Maurice J. Zardus, Jr., Box 89, La Barge, Wyo., all by C. V. Duff; Ervil D. Clark, Pacific Union College, Angwin, Calif., by Donald V. Hemphill; William L. Brown, 173 Hillhurst Blvd., Toronto, Ontaro, Canada, and Kai Curry-Lindahl, Director, Zoological Dept., Nordiska Museet and Skansen, Stockholm, Sweden, by Thomas R. Howell; Keith S. Brown, Jr., Fleming House, California Inst. Tech., 1301 E. California St., Pasadena, Calif., and Robert J. Drake, Dept. Zoology, Univ. Arizona, Tucson, Ariz., by Joe T. Marshall, Jr.; S. Craig Smith, 2 So. Clinton St., Poughkeepsie, N.Y., by Alden H. Miller; Richard Holmes, Nelson Hall, Humboldt State College, Arcata, Calif., and William Sharp, 11128 82nd Ave., Edmonton, Alberta, Canada, by Jack C. von Bloeker, Jr.; and A. R. Tribe, Forest Office, Hargeisa, Somaliland Protectorate, Africa, by John G. Williams.

Kenneth Stager announced that a Dr. Cadcott is conducting a research project in the Los Angeles area on the effects of smog on animals and especially on birds.

C. V. Duff presented the report of the nominating committee. The following slate of officers for 1957 was elected: Thomas R. Howell, President; M. Dale Arvey, First Vice-president; Henry E. Childs, Jr., Second Vice-president; and Dorothy E. Groner, Secretary.

The speaker of the evening was Dr. Richard M. Straw, whose topic was "Flower Birds and Bird Flowers."—CAROLYN MURPHEY SMITH, *Acting Secretary.*

COOPER ORNITHOLOGICAL SOCIETY
STATEMENT OF CASH RECEIPTS AND DISBURSEMENTS
FOR THE YEAR ENDING DECEMBER 31, 1956

CASH IN BANK, December 31, 1955			$ 8,983.31
ADD: CASH RECEIPTS			
General Publication Fund			
Membership dues, regular and sustaining	$4,813.83		
Subscriptions for the Condor	941.72		
Condor sales	126.62		
Phonograph record sales (4 records sold)	30.00		
Dividends and interest received on endowment funds invested (Note A)	3,780.49		
Contributions received for the publication of the Condor	1,050.00		
Other cash receipts	14.44	$10,757.10	
Avifauna Fund			
Avifauna sales, net (Note B)	1,054.83		
Contribution received	500.00		
Other cash receipts	20.06	1,574.89	
Endowment Fund			
Life memberships and installment payments received on life memberships	540.00		
Contributions	1,100.00		
Other cash receipts	629.00	2,269.00	14,600.99
			23,584.30
DEDUCT: CASH DISBURSEMENTS			
General Publication Fund			
Publication costs of The Condor			
Printing	8,870.84		
Engraving	1,853.86		
Purchase of back issues	2.00	10,726.70	
Cost of phonograph records		5.50	
Administrative expenses			
Northern division	72.96		
Southern division	54.65		
Annual meeting	192.59		
Business manager	303.80		
Assistant business manager	50.00		
Treasurer	364.73		
Editor	462.00		
Other disbursements	30.81	1,531.54	
Avifauna Fund			
Sales tax	1.80		
Drawings	660.00		
Printing	474.99		
Other disbursements	148.07	1,284.86	
Endowment Fund			
Purchase of corporate stock	2,563.32	2,563.32	16,111.92
CASH IN BANK, December 31, 1956			$ 7,472.38

	December 31, 1955	December 31, 1956
CASH IN BANK ALLOCATED TO FUNDS AS FOLLOWS:		
General Publication Fund	$6,851.74	$5,345.10
Avifauna Fund	1,757.11	2,047.14
Endowment Fund (to be invested)	374.46	80.14
	$8,983.31	$7,472.38

NOTE A: At December 31, 1956, the business manager had in his custody endowment funds invested in corporate stocks which cost $45,802.81 and had a market value of $95,971.45. This endowment fund includes contributions received in the names of Florence M. Bailey, Louis B. Bishop, Albert E. Colburn, Joseph Grinnell, A. Brazier Howell, Harry R. Painton and Isabel A. Thomson.

NOTE B: At December 31, 1956, the Society had a stock of Avifaunas for which the total of quoted list prices was $28,642.50.

C. V. DUFF, *Business Manager*

PREPARATION OF MANUSCRIPTS FOR THE CONDOR

Articles published in the Condor normally are written by members of the Cooper Ornithological Society. Practically all the Society's money goes into the journal; no editor or business manager receives any pay other than the satisfaction of doing a service worthily. The preparation of good copy by the author will contribute greatly to accuracy of published output, dispatch in handling, and economy of production.

To be acceptable for inclusion in the Condor, articles must not duplicate in any substantial way material that is published elsewhere. Any type of subject bearing on birds may be considered; but the geographic areas of primary concern are western North America, Central America, and the Pacific Basin. Manuscripts may be sent to the editors at the Museum of Vertebrate Zoology. Proofs with edited manuscripts will be sent to authors, at which time reprints may be ordered.

In the interests of accuracy and economy, observe the following: do not duplicate data in text, tables, or charts; check citations to original sources and verify text references; quoted statements must be exact replicas of the original; preferably use vernacular names applicable to the entire avian species (for a guide in this regard, see "The Distribution of the Birds of California," Pac. Coast Avif. No. 27, 1944:5–34); in general, avoid subspecific vernaculars; insert scientific names for species but not the subspecific name except in taxonomic papers or where the race concerned has been critically determined by the author or his collaborators; revise the manuscript repeatedly to remove superfluous words and phrases, immaterial detail, and repetitious statements.

Note Condor style and usage. "General Articles" and the "Field and Study" items are set up in different form. Provide a concise, meaningful title, and, where needed, subtitles within the text. Footnotes are not used. The address line may serve to indicate institutional connection, and to it should be added the date of transmittal of the manuscript. Terminal bibliographies are desirable where five or more titles are to be cited; otherwise, the references may be included in the text. For bibliographic style, note closely the practices employed in recent volumes of the journal. A factual summary is recommended for longer papers.

Rules for copy.—(1) Typewrite material, using one side of paper only; (2) double space all material and leave liberal margins; (3) use 8½ × 11 inch paper of standard weight (avoid onion skin); (4) carbon copies are not acceptable; (5) place tables on separate pages; (6) number pages in upper right hand corner.

Illustrations.—Photographs should be glossy prints of good contrast. Make line drawings with India ink; plan linework and lettering for at least ½ reduction; do not use typewritten labels on the face of the drawing. Provide typed legends on separate sheets.

Helpful references on writing: Manual of Style, University of Chicago Press, and Rules of the Editorial Committee, University of California Press. On scientific nomenclature: A.O.U. Check-list (with supplements 19 through 30) and Pacific Coast Avifauna No. 27; authors are not required to follow either of these works.